QH
1
C213
NH

The CANADIAN FIELD-NATURALIST

Published by THE OTTAWA FIELD-NATURALISTS' CLUB, Ottawa, Canada

Volume 117, Number 1

January–March 2003

The Ottawa Field-Naturalists' Club

FOUNDED IN 1879

Patrons

Her Excellency The Right Honourable Adrienne Clarkson, C.C., C.M.M., C.D.
Governor General of Canada
His Excellency John Ralston Saul, C.C.

The objectives of this Club shall be to promote the appreciation, preservation and conservation of Canada's natural heritage; to encourage investigation and publish the results of research in all fields of natural history and to diffuse information on these fields as widely as possible; to support and cooperate with organizations engaged in preserving, maintaining or restoring environments of high quality for living things.

Honorary Members

Edward L. Bousfield
Donald M. Britton
Irwin M. Brodo
William J. Cody
Francis R. Cook
Ellaine Dickson
Bruce Di Labio
R. Yorke Edwards
Anthony J. Erskine
John M. Gillett
C. Stuart Houston
George F. Ledingham
John A. Livingston
Stewart D. MacDonald
Hue N. MacKenzie
Theodore Mosquin
Eugene G. Munroe
Robert W. Nero
E. Franklin Pope
William O. Pruitt, Jr.
Joyce and Allan Reddoch
Mary E. Stuart
John B. Theberge
Sheila Thomson

2003 Council

President: Garry McNulty

Vice-President: Mike Murphy
Gillian Marston

Recording Secretary: Susan Laurie Bourque

Treasurer: Frank Pope

Past President: Eleanor Zurbrigg

Ronald E. Bedford
Rosanne Bishop
John Cameron
Janet Castle
Charlie Clifford
William J. Cody
Kathy Conlan
Francis R. Cook
Barbara Gaertner
Marcel Gahbauer
Diane Lepage
Karen McLachlan Hamilton
David Hobden
Cendrine Huemer
Roy John
Stanley Rosenbaum
Louise Schwartz
David Smythe
Chris Traynor
Dorothy Whyte

To communicate with the Club, address postal correspondence to: The Ottawa Field-Naturalists' Club, Box P.O. Box 35069, Westgate P.O. Ottawa, Canada K1Z 1A2, or e-mail: ofnc@achilles.net.
For information on Club activities telephone (613) 722-3050 or check http//www.achilles.net/ofnc/index.htm

The Canadian Field-Naturalist

The Canadian Field-Naturalist is published quarterly by The Ottawa Field-Naturalists' Club. Opinions and ideas expressed in this journal do not necessarily reflect those of The Ottawa Field-Naturalists' Club or any other agency.

We acknowledge the financial support of the Government of Canada toward our mailing cost through the Publication Assistance Program (PAP), Heritage number 09477.

Editor: Dr. Francis R. Cook, R.R. 3, North Augusta, Ontario K0G 1R0; (613) 269-3211; e-mail: fcook@achilles.net
Copy Editor: Elizabeth Morton
Business Manager: William J. Cody, P.O. Box 35069, Westgate P.O. Ottawa, Canada K1Z 1A2 (613) 759-1374
Book Review Editor: Dr. J. Wilson (deceased 23 June 2003)

Associate Editors:

Robert R. Anderson
Charles D. Bird
Robert R. Campbell
Paul M. Catling
Brian W. Coad
Anthony J. Erskine
David Nagorsen
Donald F. McAlpine
William O. Pruitt, Jr.

Chairman, Publications Committee: Ronald E. Bedford

All manuscripts intended for publication should be addressed to the Editor and sent by postal mail. Book Review correspondance should be addressed to Ottawa Field Naturalists' Club, Box 35069, Westgate P.O., Ottawa, Canada K1Z 1A2

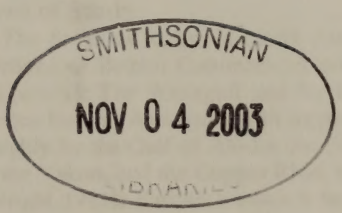
Subscriptions and Membership
Subscription rates for individuals are $28 per calendar year. Libraries and other institutions may subscribe at the rate of $45 per year (volume). The Ottawa Field-Naturalists' Club annual membership fee of $28 (individual) $30 (family) $50 (sustaining) and $500 (life) includes a subscription to *The Canadian Field-Naturalist.* All foreign subscribers and members (including USA) must add an additional $5.00 to cover postage. The club regional journal, *Trail & Landscape*, covers the Ottawa District and Local Club events. It is mailed to Ottawa area members, and available to those outside Ottawa on request. It is available to Libraries at $28 per year. Subscriptions, applications for membership, notices of changes of address, and undeliverable copies should be mailed to: The Ottawa Field-Naturalists' Club, P.O. Box 35069, Westgate P.O. Ottawa, Canada K1Z 1A2. Canada Post Publications Mail Agreement number 40012317. Return Postage Guaranteed. Date of this issue: January–March 2003. (September 2003).

Cover: Purple Loosestrife, *Lythrum salicaria* infestation in the Netley-Libau Marsh, Manitoba, in 2001. Photograph courtesy of Cory J. Lindgren. See article pages 100–109.

THE CANADIAN FIELD-NATURALIST

Volume 117

2003



THE OTTAWA FIELD-NATURALISTS' CLUB

OTTAWA CANADA

The Canadian Field-Naturalist

Volume 117, Number 1 January-March 2003

Birds and Mammals of the St. Elias Mountain Parks: Checklist Evidence for a Biogeographic Convergence Zone

RYAN K. DANBY

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9 Canada (rdanby@ualberta.ca)

Danby, Ryan K. 2003. Birds and mammals of the St. Elias Mountain parks: checklist evidence for a biogeographic convergence zone. Canadian Field-Naturalist 117(1): 1-18.

The St. Elias region of North America occupies portions of British Columbia, Alaska, and Yukon and consists of a contiguous network of protected areas. Available information on avian and mammalian diversity in each of the region's five major protected areas (Kluane National Park, Wrangell-St. Elias National Park and Preserve, Glacier Bay National Park and Preserve, Tatshenshini-Alsek Provincial Park, and Tetlin National Wildlife Refuge) was integrated to create a species checklist as part of an ongoing effort to create a region-wide ecological database for research and management purposes. Based on the tabulated data, the five protected areas combine to protect a total of 178 species of breeding birds and 51 species of terrestrial mammals. These numbers indicate a level of richness up to 30% beyond that predicted at a continental scale. A high proportion of species near their distributional limits and typical of several different biogeographic provinces appears to account for this value and supports consideration of the region as a biogeographic convergence zone.

Key Words: species checklist, biogeography, convergence zone, tension zone, Glacier Bay, Kluane, Tatshenshini-Alsek, Tetlin, Wrangell-St. Elias, Alaska, British Columbia, Yukon.

A list of species present within a given geographic area, commonly referred to as a checklist, is among the most basic types of information available to a biologist. Checklists have long been used as a central component in biogeographical description and continue to act as the fundamental source in documenting species distribution. However, they have an inherent drawback which can render them undesirable for certain applications. Most checklists are both spatially and temporally unstandardized, thereby preventing all but the most simple statistical analyses. Despite this limitation, they are valuable tools in biogeographical analysis and species distribution mapping, particularly when examining broader spatial and temporal scales (Miller 1994; Droege et al. 1998).

As part of an ongoing effort to create a region-wide ecological database for the St. Elias region (Danby 1999), available data on avian and mammalian diversity in each of the region's five main protected areas — Kluane National Park, Wrangell-St. Elias National Park and Preserve, Glacier Bay National Park and Preserve, Tatshenshini-Alsek Provincial Park, and Tetlin National Wildlife Refuge — was integrated into a regional checklist. The checklist was then analyzed with a view to assessing similarities between the bird and mammal fauna of the five areas and identifying the broad biogeographical influences on species diversity and distribution in the region. This paper presents the methodology used in this endeavour, the list which was produced, and the analysis which followed.

Area of Study

The St. Elias region of North America occupies portions of British Columbia, Alaska, and Yukon (Figure 1). The Wrangell and St. Elias mountain ranges form its backbone, with its perimeter marked roughly by the Gulf of Alaska, the Shakwak Trench in the Yukon, and the Copper River valley in Alaska (Wright 1981). Elevation extends from sea level to 5959 m (Schmidt 1992) and the region is the source of several large watersheds, including the Tatshenshini-Alsek, Chitina-Copper, and Tanana, and it contains the largest temperate icefield in the world (Theberge 1980). Northern coniferous or boreal forests characterized by White and/or Black spruce (*Picea glauca, P. mariana*) predominate the interior lowlands and montane valleys, while forests of Sitka Spruce (*P. sitchensis*), and Western and Mountain hemlock (*Tsuga heterophylla, T. mertensiana*) are predominant in coastal areas. Forests give way to subalpine zones of tall shrubs at higher elevations which, in turn, give way to alpine meadows, tundra, and permanent snow and ice at the highest elevations.

Much of the St. Elias region consists of a network of public lands and protected areas managed by a

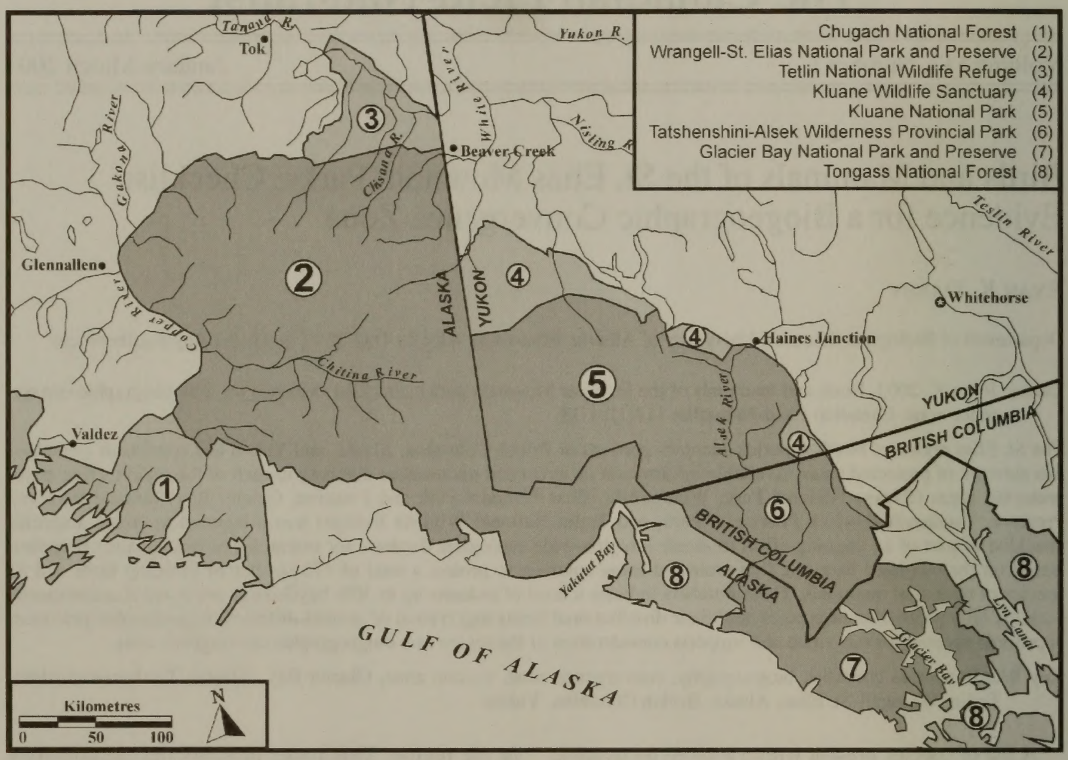


Figure 1. The St. Elias Mountain Parks. Darker shading indicates the core protected zone that comprises the World Heritage Site.

variety of federal, state, provincial, and territorial agencies. It is, in essence, one continuous protected area with Wrangell-St. Elias and Glacier Bay National Parks and Preserves in Alaska, Kluane National Park and Reserve in the Yukon Territory, and Tatshenshini-Alsek Provincial Park in British Columbia forming its core. In total these four parks protect 98 300 km^2 and combine to form the largest UNESCO World Heritage Site (Danby and Slocombe 2002). In addition to these four core areas there are several other peripheral protected areas, including Tetlin National Wildlife Refuge, Chugach and Tongass National Forests, Kluane Wildlife Sanctuary, and Chilkat Bald Eagle Preserve (Figure 1).

Methods

Information pertaining to each of the four core protected areas in the St. Elias region, as well as the Tetlin National Wildlife Refuge, was integrated to create a standardized, region-wide checklist of birds and mammals previously recorded within each area. Relative abundance was not included because presence of a species was the only information which was common to all information sources. Analysis of the checklist was carried out with a view to characterizing the region's broad biogeographical nature.

The list was generated by combining information from numerous different sources. This task was, however, not as straightforward as initially expected. While each of the five protected areas maintain species checklists, they are in different formats and categorize the status of species quite differently. Moreover, taxonomic nomenclature differs amongst available information. Ways of overcoming these challenges are particularly notable since they are indicative of the difference between simply tabulating existing data and the more complex task of integrating available data and information (see Slocombe 2001).

Taxonomic standardization was the first crucial step in information integration. The American Ornithologists' Union (AOU) *Checklist of North American Birds* (1998) is the standard authority for avian taxonomy in North America and was used here. The seventh edition and its supplements were used. The compendium of North American mammal biology produced by the American Society of Mammalogists (Wilson and Ruff 1999) was used in standardizing mammalian taxonomy. The marine

mammals (pinnipeds, cetaceans, and the Sea Otter, *Enhydra lutris*) were not included.

Relative abundance was not included as part of the list since it was not available for all species or each of the protected areas. While some sources provided detailed information on habitats, relative abundance, and historical accounts, others indicated only whether a species had been observed within a particular area. Although desired, it was not possible to generate a standardized account of abundance for each species in each of the five areas from this information.

A species of bird was included on the list only when a confirmed observation had been made within the boundaries of the respective protected area. Residency and breeding status of birds were assessed using the categories in Table 1. Because of variability in how the residency of mammals has been classified in each of the protected areas, as well as conflicting reports among different sources, mammals were categorized as definitely occurring, likely occurring, or possibly occurring. "Definite" species have been trapped within a given area or have been observed by a reputable individual with sufficient documentation provided. "Likely" species are definite in adjacent areas but have not been confirmed within the borders of the given area, even though suitable habitat exists. Criteria for "possible" species varied for each area, but were generally based on habitat suitability and relative abundance in adjacent areas. The process and sources used in assigning species from each protected area to the list were as follows:

Glacier Bay National Park and Preserve

The park's mammal checklist (Taylor 1984*) was used as the template for species occurrence with MacDonald and Cook (1996) used to bring this list up to date and help differentiate between likely and possible occurrences when confirmed observations were absent. Paige (no date*) served as the template for bird species occurrence, and was supplemented by accounts from park staff. Any bird denoted with the symbols for "nests or unfledged young found" or "nesting suspected" was marked as breeding or probably breeding within the park, respectively. A species which occurs regularly during the breeding season but where breeding has not been confirmed — despite the fact that suitable breeding conditions exist—was assigned as a potential/possible breeder. Armstrong (1990) was used as a reference to determine whether or not a species should be considered a potential breeder or an incidental/casual visitor to the park.

Tatshenshini-Alsek Provincial Park

Lofroth and Mahon (1993*) provided the basic species list for mammals and birds in Tatshenshini-Alsek Provincial Park. This report, based on field

TABLE 1. General classification used in integrating accounts of bird status.

B – Confirmed breeding within park boundaries
A species was assigned to this category when breeding has been confirmed within the park boundaries through observations related to nesting activities and/or observation of recently fledged young.

b – Probably breeding within park boundaries
A species was assigned to this category when breeding is highly probable but nests or fledged young have yet to be positively identified.

(b) – Potential breeding within park boundaries
A species was assigned to this category if it has been observed residing within a park during its breeding period and suitable breeding habitat is known to exist.

m – Migrant
A species was classified as a migrant if it regularly utilizes the park during migration to and/or from breeding grounds.

p – Palaegic species often seen near or on shore
Palaegic species not known to breed within a park but often observed near shore were assigned to this category.

w – The park is distinct winter habitat for a species
Long and short distance migrants regularly utilizing a park as part of its winter range, but not suspected to breed, were assigned to this category.

i/c – Incidental record/Casual wanderer
This category was reserved for irregularly occurring species. Species placed in this category range from those occasionally observed within a park to accidental species far from the core of their global range. In any case, there are a limited number of sightings of the species and the park is located outside of its known breeding range. As such, they are not suspected of breeding within the park.

? – Status unknown
As with all other species on the regional checklist, species placed in this category have been positively identified within a park's boundaries. However, the specific park is not located within the species' known breeding range and not enough information is available on frequency or regularity of occurrence to accurately assign it to another category.

surveys undertaken during the summer of 1992, summarized all other occurrences previously noted for the park. When definite occurrence of a mammal was not confirmed, likely and possible occurrences were differentiated by cross-checking with range maps in Wilson and Ruff (1999) as well as the collection locations mapped in Youngman (1975).

Campbell et al. (1990a, 1990b, 1997, 2001) served as a supporting reference for additional bird breeding accounts. However, due to its remote location and more recent establishment (1993), breeding status has been confirmed for only a small number of species in Tatshenshini-Alsek. Where confirmed breeding records were absent, but the park is located within a species' known continental breeding range (based on range maps by Godfrey 1986) *and* the species was noted as being common in suitable breeding habitat by Lofroth and Mahon (1993*), it was assigned to the "probable breeder" category. Birds were categorized as being "potential" breeders if they had been observed within the park during breeding season, suitable breeding habitat exists within the park, and the park falls within the breeding range described by Godfrey (1986). The lack of records for migrants and the higher number of species categorized as "status unknown" can be explained by the fact that most observations in the Tatshenshini-Alsek area have been during the breeding season.

Kluane National Park

Gray (1987*) developed an annotated checklist of birds for Kluane National Park based on all prior avian studies conducted in the area as well as range maps provided by Godfrey (1966). Species were categorized as positively breeding, probably breeding, migrant, or wanderer. However, examination of the annotations indicates that many of the breeding categorizations are actually based on observations made in the adjacent Kluane Wildlife Sanctuary. Several modifications were therefore made to Gray's list in order to confine records specifically to Kluane National Park. Where breeding has been confirmed in the Sanctuary but not in the Park, the status of a species was dropped to *probable* or *potential* breeder. The differentiation between these two categories was made on the basis of relative abundance. When Gray noted a species as common, abundant, or frequent within the National Park, the species was considered a probable breeder. When a species was considered occasional or rare, yet breeding had been confirmed within the Sanctuary or immediately outside the Park, the species was categorized as a potential breeder within the park.

Checklists by Gray (1987*), Parks Canada (1984*), and Krebs and Wingate (1976) were used to develop the list of mammals observed in Kluane with careful attention given to differentiating between species observed within the areas originally part of the Kluane Game Sanctuary but not currently included inside the National Park. Youngman (1975) and relevant sources therein were used to differentiate between likely and possible occurrences.

Wrangell-St. Elias National Park and Preserve

The Alaska Natural History Association's (ANHA) checklist of birds (1993*) is the only list of birds previously compiled for the Wrangell-St. Elias area. Although it lists the relative abundance of individual species in different locations within the Park at different times of the year, it does not indicate breeding status for any of these species. Subsequent searches revealed that confirmed breeding reports for Wrangell-St. Elias are limited. All information on confirmed breeding was obtained from park biologists.

A species was considered a probable breeder when the ANHA checklist considered it to be common in the Park and Armstrong (1990) and Dunn (2002) identified the Park within the species' breeding range in Alaska. Potential breeders were identified as those whose breeding range coincided with the Park (as identified by Armstrong 1990 and Dunn 2002) but were classified as uncommon or rare on the ANHA checklist.

Checklists provided by park staff (Gravier 1997*; Cook and MacDonald 2002*) were used to assess the status of mammalian species. When definite occurrence was not confirmed, likely and possible occurrences were differentiated by cross-checking with range maps in Wilson and Ruff (1999) as well as the collection locations of voucher specimens housed at the University of Alaska Museum.

Tetlin National Wildlife Refuge

The Refuge checklist of birds (Doyle 1996*) was used as a template for species occurrence. While the list lumps confirmed breeders and probable breeders together, a list of confirmed breeders within Refuge boundaries was obtained from Refuge biologists. Species suspected to breed in the Refuge, but without positive confirmation of breeding, were then assessed by relative abundance. Those classified as uncommon or rare were considered potential breeders; those classified as common were considered probable breeders. Those species noted as year-round residents on the Refuge checklist were assigned to the probable breeding category if breeding has yet to be confirmed, regardless of their relative abundance.

A checklist provided by refuge staff (Doyle 1996*) was used to assess the status of mammals. Updates to the list, based on recent small mammal trapping, were provided by refuge staff. Likely occurrences were differentiated from possible occurrences by cross-checking with range maps in Wilson and Ruff (1999) as well as the collection locations of voucher specimens housed at the University of Alaska Museum.

Results and Analysis

Species Richness

The regional checklist is presented in Appendix A (birds) and Appendix B (mammals). Based on these data, the four St. Elias Mountain Parks and the Tetlin Refuge combine to protect a total of 178 species of confirmed, probable, and potential breeding birds, with an additional 89 species confirmed, but not suspected to breed. Forty-eight species of terrestrial mammals have been confirmed within the protected area complex, with three additional species suspected. Table 2 summarizes the number of species in each area. Tables 3 and 4 summarize the number of species shared amongst the protected areas as well as the similarities between areas.

Differences between the fauna of coastal and interior regions are clearly illustrated by the Jaccard similarity indices (Connor and McCoy 1979) presented in Tables 3 and 4. Based on a relative scale from zero to one, Glacier Bay National Park and Preserve

TABLE 2. Bird and mammal species richness in the St. Elias Mountain Parks.

Protected Area	Area (km^2)	Number of Species			
		Breeding Birds[1]	Total Birds[2]	Confirmed Mammals[3]	Total Mammals[4]
Kluane	22013	131	168	39	45
Wrangell-St. Elias	53420	146	181	36	42
Glacier Bay	13355	108	223	29	29
Tatshenshini-Alsek	9580	131	162	31	39
Tetlin	3739	119	186	29	40
Total Species	102107	178	267	48	51

[1] Confirmed, probable, and possible breeders.
[2] Total species; breeders and otherwise.
[3] Species confirmed within protected area boundaries; excludes incidentals.
[4] Total species; confirmed, likely, possible and incidental.

TABLE 3. Number of bird species (confirmed, probable, and possible breeders) common to or shared between protected areas (top/right). Bottom/left of matrix lists indices of similarity using Jaccard's coefficient. Matrix diagonal lists the number of species not found in the other four areas.

	Kluane	Wrangell-St. Elias	Glacier Bay	Tatshenshini-Alsek	Tetlin
Kluane	**1**	118	78	119	107
Wrangell-St. Elias	0.74	**4**	95	116	109
Glacier Bay	0.48	0.6	**9**	84	68
Tatshenshini-Alsek	0.83	0.72	0.54	**2**	101
Tetlin	0.75	0.7	0.43	0.68	**6**

TABLE 4. Number of terrestrial mammal species (confirmed and likely residents) common to and/or shared between protected areas (top/right). Bottom/left of matrix lists indices of similarity using Jaccard's coefficient. Matrix diagonal lists the number of species not found in the other four areas.

	Kluane	Wrangell-St. Elias	Glacier Bay	Tatshenshini-Alsek	Tetlin
Kluane	**1**	37	28	29	31
Wrangell-St. Elias	0.79	**2**	26	33	31
Glacier Bay	0.64	0.59	**1**	26	23
Tatshenshini-Alsek	0.8	0.75	0.67	**0**	26
Tetlin	0.7	0.74	0.61	0.67	**0**

has the lowest average similarity indices for both bird and mammal assemblages. It is also evident from these indices, as well as examination of the species list, that areas immediately adjacent to each other generally have more similar faunas than those separated by one or more areas.

Differences in species richness among the five areas can be attributed to several factors. For example, size and habitat diversity as factors are evident in Tetlin Refuge, which has fewer species than its closest neighbours. It is the smallest of the five areas and is composed largely of boreal forest, with very little of the mountainous terrain that characterizes the four other areas. But not all differences can be attributed to habitat diversity. For example, the slightly lower number of confirmed species in the Tatshenshini-Alsek is likely a function of the recent establishment of this park and the fact that biodiversity inventory and scientific investigation have been limited in comparison to the other areas. The lower number of species — particularly mammals — recorded in Glacier Bay National Park may be related to the fact that this entire area was under glacial ice until just over 200 years ago (Mann 1986). While recolonization of the area by larger mammals with greater dispersal capabilities has occurred, some species with limited dispersal capabilities — but found elsewhere in southeast Alaska (for example, *Zapus hudsonius, Z. princeps,* and *Synaptomys borealis*) — have yet to be recorded in the Park.

When considered as a single unit, the number of terrestrial mammals as well as breeding birds in the St. Elias region exceeds previously reported values modelled on continental patterns of species diversity. For example, an examination of maps contained in Brown and Lomolino (1998) indicates that the St. Elias region should support between 120 and 150 breeding birds, while the number of mammals it supports should be in the range of 40 to 45 species. Using these two estimates as guidelines, it appears that the St. Elias Mountain Parks support roughly 10 to 30 percent more species than expected. Given that this paper excludes consideration of species present in adjacent unprotected areas, the actual number for the entire St. Elias region (i.e., protected and unprotected areas) is likely to approach the upper limit of this range.

Centres of Biogeographic Influence

Examination of the species list indicates that the St. Elias region is influenced by several major biogeographic regions and sub-regions. As illustrated in

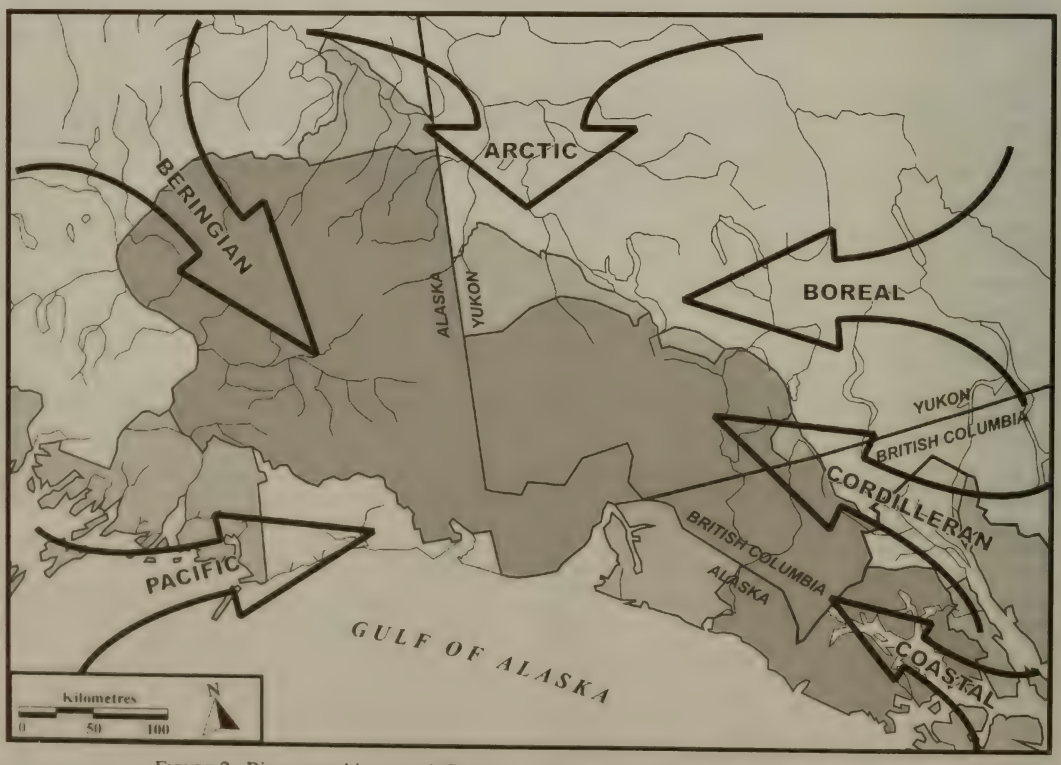


FIGURE 2. Biogeographic zones influencing species composition of the St. Elias region.

Figure 2, this includes species typical of arctic, boreal, cordilleran, and coastal ecosystems as well as species, subspecies and varieties theorized to have evolved in the Pleistocene Beringian refugium of central Yukon and Alaska. As shown in Table 5, several of these species occur at or near their distributional limits in the St. Elias region, indicating that the region is located at the confluence of these biogeographic zones. This confluence or "convergence zone" differs from the more commonly used "tension zone" in that the latter is typically used to refer to the transition between two biogeographic regions or provinces. The convergence model presented here refers to three or more biogeographic zones coming together from several different directions, and therefore extends beyond the notion of a transition. "Biogeographic crossroads" is an alternative term proposed by Spector (2002).

In addition to species occurrences supporting the model in Figure 2 are the occurrences of major mammalian subspecies within the five protected areas. Based on a classification by Nowak (1996), the range of two of North America's subspecies of Gray Wolf (*Canis lupus nubilus* and *C. l. occidentalis*) converge in the greater St. Elias region. A sixth subspecies, *C. l. ligoni* (Person et al. 1996), inhabits parts of southeast Alaska. Similarly, of the four recognized subspecies of Moose (*Alces alces*) in North America, two are present in the greater St. Elias region. *A. a. gigas* is the largest subspecies of Moose known and appears to have evolved during the Wisconsin ice age in the ice-free area of north-central Yukon and Alaska. *A. a. andersoni* moved northwards with the retreat of the continental ice mass and reaches its northern limits in southern Yukon. The southwest Yukon represents a transition zone

TABLE 5. Evidence for the St. Elias region as a biogeographic tension zone. Species listed here are at or very near their distributional limits in the St. Elias region. Widely recognized subspecies are shown with scientific name. Nomenclature follows that of the checklists in Appendicies A and B.

Distribution Type	Terrestrial Mammals[1]	Breeding Birds[2]
Northern Limit of Range (typically of Cordilleran association)	Northwestern Deer Mouse, Alexander Archipelago Wolf *(Canis lupus ligoni)*, Cougar, Mule Deer, Mountain Goat	Blue Grouse, Rufous Hummingbird, Red-breasted Sapsucker, Pacific-slope Flycatcher, Dusky Flycatcher, Stellar's Jay, Northwestern Crow, Chestnut-backed Chickadee, Mountain Bluebird, Townsend's Warbler, MacGillvary's Warbler, Western Tanager
Southern or Southeastern Limit of Range (typically of Arctic association; mammals typically of Beringian origin)	Tundra Shrew, Tiny Shrew, Collared Pika, Alaska Marmot, Arctic Ground Squirrel, Northern Red-backed Vole, Singing Vole, Tundra Vole, Brown Lemming, Barren-ground Caribou (*Rangifer tarandus granti*), Alaskan Moose (*Alces alces gigas*), Dall Sheep (*Ovis dalli dalli*)	Red-throated Loon, Long-tailed duck, Gyrfalcon, Surfbird, Least Sandpiper, Red-necked Phalarope, Parasitic Jaeger, Aleutian Tern, Northern Shrike, Arctic Warbler, Common Redpoll
Western Limit of Range (typically of Boreal association)	Eastern Heather Vole, Boreal Gray Wolf (*Canis lupus occidentalis*), Woodland Caribou (*Rangifer tarandus caribou*)	Greater Yellowlegs, Yellow-bellied Sapsucker, Red-breasted Nuthatch, Tennessee Warbler, Purple Finch
Northwestern Limit of Range (typically central Continental origin)	American Water Shrew, Least Chipmunk, Woodchuck, Deer Mouse, Bushy-tailed Woodrat, American Bison[3]	Great-blue Heron, Gadwall, Hooded Merganser, Red-tailed Hawk, Sora, Killdeer, Common Nighthawk, Barn Swallow, Brown Creeper, Golden-crowned Kinglet, American Redstart, Common Yellowthroat, Chipping Sparrow, Song Sparrow, Red-winged Blackbird
Other	Long-tailed Vole[4], Taiga Vole[4]	Redhead[3], Ring-necked Duck[3], Brewer's Sparrow[3], Lapland Longspur[3], Smith's Longspur[3], Snow Bunting[3]

[1]Based on range maps in Wilson and Ruff (1999), Chapman and Feldhamer (1982), and Hall (1981).
[2]Based on range maps in Dunn (2002).
[3]Disjunct, regional, or isolated populations. See Peek et al. (1987) for a discussion as to whether or not Wood Bison has been introduced or re-introduced.
[4]Species is at edge of continental range, but biogeographic association remains unclear.

between the ranges of the two subspecies (Franzmann and Schwartz 1998).

The notion of the St. Elias region as a zone of biogeographic convergence is not new. Previous authors to advance this concept include Cameron (1952), Drury (1953), Theberge (1974*), Krebs and Wingate (1976), and MacDonald and Cook (1996). Examinations of the geographical origins and postglacial dispersal patterns of fauna in southeast Alaska (Swarth 1936; Klein 1965; MacDonald and Cook 1996) and in the Yukon (Youngman 1975) also support the existence of a biogeographic convergence zone. However, each of these authors has examined only a portion of the entire St. Elias region and most have focussed on either mammals or birds, not both. When the region is examined as a collective whole, and when multiple taxa are considered, this characteristic becomes far more apparent.

Previous botanical inventories within the St. Elias region also support the biogeographic convergence model. This includes studies of Kluane National Park (Douglas 1980*), Wrangell-St. Elias (Cook and Roland 2002), and Tatshenshini-Alsek (Pojar 1993*). More general floristic examinations of Alaska (Hultén 1968) and Yukon (Cody 1996) also support the model from a botanical perspective. A preliminary plant checklist of the four core protected areas of the St. Elias region has been assembled (Danby 1999), but taxonomic standardization and biogeographic analysis have yet to occur.

Physical Influences

The continental position of the St. Elias region combined with a complex glacial history plays a prominent role in the existence of the biogeographic convergence zone. Several other factors act to maintain the zone, and the interplay between macroclimate and physiography appears to play a significant role in this respect. The St. Elias region spans two broad climatic zones, each characterized by two very different temperature and precipitation regimes (Wahl et al. 1987). In addition, the region is situated at the meeting point of several of North America's major tectonic terranes (Silberling et al. 1992) and contains the confluence of several major mountain ranges and intermountain troughs (Bostock 1948). In combination, these physical factors create substantial variability in the region's landscape, allowing for a diverse array of habitats and, therefore, species for such a northern latitude.

This interplay among physical factors is quite complex and occurs at a variety of scales. For example, the valleys of the Alsek and Copper rivers sever the physical and climatic barrier created by the high coastal mountains, funnelling warm moist air from the Gulf to the interior and acting as corridors for the movement of species from the coast to the interior, and vice versa (Danby 1999). At finer scales, topographic variability results in increased habitat diversity by creating local microclimates associated with differences in altitude, slope, and aspect.

Discussion and Conclusion

Checklists are often spatially and temporally unstandardized, precluding all but very simple statistical analysis and invoking the perception that they are relatively useless in scientific studies. While these perceived limitations may be valid at the site and landscape scales, checklists remain one of the most fundamental tools available in any regional biogeographical analysis (Droege et al. 1998). The value of such an approach has been illustrated elsewhere (e.g., Erskine and Stein 1964) and is demonstrated here with evidence supporting the biogeographic model of convergence previously hypothesized for single taxa and/or individual parks within the entire St. Elias protected area complex.

Despite this potential utility, issues still remain in their creation and use. Taxonomic standardization is likely the first issue the compiler will face — due largely to changes in classification and nomenclature over time — and must be addressed immediately in order for successful data integration to occur. Similarly, given that nearly all checklists compiled at this scale will utilize numerous different sources, it is essential that accuracy is maintained during the integration process and that a systematic method is utilized in assessing species status. Recognizing, and stating, the limitations of the checklist is equally important. This is amplified considerably when annotations are not detailed and there is little or no information on the relative abundance of a species.

This concern is readily apparent with the mammal portion of the checklist presented here. Although it lists all mammals positively identified within each of the protected areas, it provides little information on the status of the species within each park. For example, Mule Deer are rare in Kluane but sightings are increasing as they extend their range northwards (Hoefs 2001) and they can no longer be considered "incidental". However, this is not evident to the checklist user. Similarly, the Tiny Shrew (*Sorex yukonicus*) (Dokuchaev 1997) is known to the region from just two specimens recently collected in Wrangell-St. Elias. More detailed annotations would obviously be helpful in these instances, but most sources did not include information detailed enough to facilitate standardized format beyond simple presence of a species.

The checklist presented here is the only list available for the entire protected area complex of the St. Elias region. It should serve as a foundation or starting point for future biological studies of the region and, as described by Theberge (1995), could be expanded to facilitate use as a tool in park planning and management. In order for this to occur it is

important that the checklist be viewed as a working database, rather than a static document. Regular review and updates are necessary, and an extension of the list to include areas adjacent to these five protected areas is warranted. Finally, initiating more detailed annotations for each species — including standardized accounts of local distribution, habitat associations, and relative abundance — will greatly improve its future utility.

Acknowledgments

Funding for this research was provided by Wilfrid Laurier University and the Canadian Department of Indian Affairs and Northern Development through the Northern Scientific Training Program. Thanks are extended to staff of the five protected areas, particularly Carl Mitchell, Mason Reid, Terry Doyle, Hank Timm, and Bud Johnson, as well as to Scott Slocombe and two anonymous reviewers who provided comments on earlier versions of the manuscript.

Documents Cited (marked * in the text)

Alaska Natural History Association (ANHA). 1993. Checklist of birds in Wrangell-St. Elias National Park and Preserve. Alaska Natural History Association, Anchorage, Alaska, and the U.S. National Park Service, Copper Center, Alaska.

Cook, J. A., and **S. O. MacDonald.** 2002. Small mammal inventory of Alaska's national parks and preserves: Wrangell-St. Elias National Park and Preserve Preliminary Summary. Report on file with U.S. National Park Service, Copper Center, Alaska.

Douglas, G. W. 1980. Biophysical inventory studies of Kluane National Park. 3 volumes. Report prepared for Parks Canada by Douglas Ecological Consultants Ltd., Victoria, British Columbia.

Doyle, T. 1996. Fish and wildlife of Tetlin National Wildlife Refuge. Unpublished data sheet on file at Tetlin National Wildlife Refuge, Tok, Alaska.

Gravier, M. E. 1997. Tetlin/Wrangell-St. Elias mammals. Unpublished checklist on file at Wrangell St. Elias National Park and Preserve, Copper Center, Alaska.

Gray, B. 1987. Kluane National Park Reserve Resource Description and Analysis. 2 volumes. Environment Canada, Parks Canada - Prairie and Northern Region, Winnipeg, Manitoba.

Lofroth, E. C., and **T. Mahon.** 1993. Vertebrate fauna observed in the Tatshenshini region of northwestern British Columbia, July 21-29, 1992. Report on file at British Columbia Ministry of Environment, Lands, and Parks, Smithers, British Columbia.

Paige, B. No Date. Birds of Glacier Bay National Park and Preserve. Alaska Natural History Association, Anchorage, Alaska, and the U.S. National Park Service, Gustavus, Alaska.

Parks Canada. 1984. Mammals of Kluane National Park. Unpublished checklist on file at Kluane National Park, Haines Junction, Yukon.

Pojar, J. 1993. Biodiversity inventory of the Tatshenshini-Alsek region. Report filed with the British Columbia Ministry of Environment, Lands, and Parks, Smithers, British Columbia.

Taylor, M. S. 1984. A mammal checklist: Glacier Bay National Park and Preserve. Alaska Natural History Association, Anchorage, Alaska.

Theberge, J. B. 1974. Survey of breeding bird abundance, Kluane National Park. Canadian Wildlife Service, Environment Canada, Edmonton, Alberta.

Literature Cited

American Ornithologist's Union (AOU). 1998. A.O.U. Checklist of North American birds. 7th edition (and supplements). American Ornithologist's Union, Washington, D.C.

Armstrong, R. H. 1990. Guide to the birds of Alaska. Alaska Northwest Books, Anchorage, Alaska.

Bostock, H. S. 1948. Physiography of the Canadian cordillera with special reference to the area north of the Fifty-fifth Parallel. GSC Memoir 247. Canadian Department of Mines and Resources, Mines and Geology Branch, Ottawa, Ontario.

Brown, J. H., and **M. V. Lomolino.** 1998. Biogeography. Sinauer Associates, Sunderland, Massachusetts.

Cameron, A. W. 1952. Notes on mammals of Yukon. Bulletin of the National Museum of Canada 126: 176–184.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, and **M. C. E. McNall.** 1990a. The Birds of British Columbia. Volume 1. Royal British Columbia Museum and Canadian Wildlife Service, Victoria, British Columbia.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, and **M. C. E. McNall.** 1990b. The Birds of British Columbia. Volume 2. Royal British Columbia Museum and Canadian Wildlife Service, Victoria, British Columbia.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, M. C. E. McNall, and **G. E. J. Smith.** 1997. The Birds of British Columbia. Volume 3. University of British Columbia Press, Vancouver, British Columbia.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, M. C. McNall, and **A. Stewart.** 2001. The Birds of British Columbia. Volume 4. University of British Columbia Press, Vancouver, British Columbia.

Chapman, J. A., and **G. A. Feldhamer.** 1982. Wild mammals of North America: Biology, management and economics. The Johns Hopkins University Press, Baltimore, Maryland.

Cody, W. J. 1996. Flora of the Yukon Territory. National Research Press, Ottawa, Ontario.

Connor, E. F., and **E. D. McCoy.** 1979. The statistics and biology of the species-area relationship. American Naturalist 113: 791–833.

Cook, M. B., and **C. A. Roland.** 2002. Notable vascular plants from Alaska in Wrangell-St. Elias National Park and Preserve with comments on the floristics. Canadian Field-Naturalist 116: 192–304.

Danby, R. K., 1999. Regional Ecology of the St. Elias Mountain Parks: A Synthesis with Management Implications. Master's thesis, Department of Geography and Environmental Studies, Wilfrid Laurier University, Waterloo, Ontario.

Danby, R. K., and **D. S. Slocombe.** 2002. Protected areas and intergovernmental cooperation in the St. Elias region. Natural Resources Journal 42: 247–282.

Dokuchaev, N. E. 1997. A new species of shrew (Soricidae, Insectivora) from Alaska. Journal of Mammalogy 78: 811–817.

Droege, S., A. Cyr, and **J. Larivee.** 1998. Checklists: an under-used tool for the inventory and monitoring of plants and animals. Conservation Biology 12: 1134–1138.

Drury, W. H. 1953. Birds of the St. Elias Quadrangle in the southwestern Yukon Territory. Canadian Field-Naturalist 67: 103-128.

Dunn, J. L. *Editor.* 2002. Field Guide to the Birds of North America. Fourth edition. National Geographic Society, Washington, D.C.

Erskine, A. J., and **R. C. Stein.** 1964. A re-evaluation of the avifauna of the Cariboo Parklands. Report of the British Columbia Provincial Museum of Natural History and Anthropology for 1963: AA18–AA35.

Franzmann, A. W., and **C. C. Schwartz.** *Editors.* 1998. Ecology and Management of the North American Moose. Smithsonian Institution Press, Washington, D.C.

Godfrey, W. E. 1966. The Birds of Canada. National Museum of Natural Sciences, Ottawa, Ontario.

Godfrey, W. E. 1986. The Birds of Canada. Revised edition. National Museum of Natural Sciences, Ottawa, Ontario.

Hall, E. R. 1981. The mammals of North America. John Wiley and Sons, New York, New York. 1181 pages.

Hoefs, M. 2001. Mule, *Odocoileus hemionus*, and White-tailed, *O. virginianus*, deer in the Yukon. Canadian Field-Naturalist 115: 296–300.

Hultén, E. 1968. Flora of Alaska and Neighbouring Territories. Stanford University Press, Stanford, California.

Klein, D. R. 1965. Postglacial distribution patterns of mammals in the southern coastal regions of Alaska. Arctic 18: 7–20.

Krebs, C. J., and **I. Wingate.** 1976. Small mammal communities of the Kluane region, Yukon Territory. Canadian Field-Naturalist 90: 379–389.

MacDonald, S. O., and **J. A. Cook.** 1996. The land mammal fauna of southeast Alaska. Canadian Field-Naturalist 110: 571–598.

Mann, D. H. 1986. Wisconsin and Holocene glaciation of southeast Alaska. Pages 237-265 *in* Glaciation in Alaska: The Geologic Record. *Edited by* T. D. Hamilton, K. M. Reed, and R. M. Thorson. Alaska Geological Society, Anchorage, Alaska.

Miller, R. I. *Editor.* 1994. Mapping the Diversity of Nature. Chapman and Hall, New York, New York.

Nowak, R. 1996. Another look at wolf taxonomy. Pages 409-416 *in* Ecology and Conservation of Wolves in a Changing World. *Edited by* L. N. Carbyn, S. H. Fritts, and D. R. Seip. Canadian Circumpolar Institute, Edmonton, Alberta.

Peek, J. M., D. G. Miquelle, and **R. G. Wright.** 1987. Are bison exotic in the Wrangell-St. Elias National Park and Preserve? Environmental Management 11: 149–153.

Person, D. K., M. Kirchoff, V. Van Ballenberghe, G. C. Iverson, and **E. Grossman.** 1996. The Alexander Archipelago Wolf: A conservation assessment. PNW-GTR-384. U.S.D.A. Forest Service, Portland, Oregon.

Schmidt, M. 1992. To the top: society team measures Mount Logan. Canadian Geographic 112: 22–35.

Silberling, N. J., D. L. Jones, J. W. H. Monger, and **P. J. Coney.** 1992. Lithotectonic Terrane Map of the North American Cordillera. U.S. Geological Survey, Denver, Colorado.

Slocombe, D. S. 2001. Integration of biological, physical, and socio-economic information. Pages 119-132 *in* A Guidebook for Integrated Ecological Assessments. *Edited by* M. E. Jensen and P. S. Bourgeron. Springer Verlag, New York, New York.

Spector, S. 2002. Biogeographic crossroads as priority areas for biodiversity conservation. Conservation Biology 16: 1480–1487.

Swarth, H. S. 1936. Origins of the fauna of the Sitkan district, Alaska. Proceedings of the California Academy of Science 223: 59–78.

Theberge, J. B. *Editor.* 1980. Kluane: Pinnacle of the Yukon. Doubleday Canada Ltd., Toronto, Ontario.

Theberge, J. B. 1995. A faunal species approach to landscape linkages. Pages 526-536 *in* Ecosystem Monitoring and Protected Areas. *Edited by* T. B. Herman, S. Bondrup-Neilson, J. H. M. Willison, and N. W. P. Munro. Science and Management of Protected Areas Association, Wolfville, Nova Scotia.

Wahl, H. E., D. B. Fraser, R. C. Harvey, and **J. B. Maxwell.** 1987. Climate of Yukon. Climatological Studies Number 40. Atmospheric Environment Services, Environment Canada, Ottawa, Ontario.

Wilson, D. E. and **S. Ruff** *Editors.* 1999. The Smithsonian book of North American mammals. UBC Press, Vancouver, British Columbia.

Wright, R. G. 1981. Wrangell-Saint Elias: international mountain wilderness. Alaska Geographic 8: 1–144.

Youngman, P. M. 1975. Mammals of the Yukon Territory. Publications in Zoology, Number 10. National Museum of Natural Sciences, Ottawa, Ontario.

Received 20 January 2000
Accepted 28 February 2003

Appendix A. Checklist of birds observed in the four St. Elias Mountain parks and Tetlin Wildlife Refuge.

WRST	Wrangell-St. Elias National Park and Preserve	B	Confirmed breeding within park boundarie
KNPR	Kluane National Park and Reserve	b	Probable breeding within park boundaries
GLBA	Glacier Bay National Park and Preserve	(b)	Potential breeding within park boundaries
TAT	Tatshenshini-Alsek Provincial Park	m	Regularly occurring migrant
TLN	Tetlin National Wildlife Refuge	p	Palaegic species often seen near or on shore
		w	The park is distinct winter habitat for a species
		i/c	Incidental record/Casual wanderer
		?	Status unknown

		WRST	KNPR	GLBA	TAT	TLN
GAVIIFORMES						
Gaviidae						
Gavia stellata	Red-throated Loon	(b)	(b)	B	B	i/c
Gavia pacifica	Pacific Loon	B	(b)	w	(b)	B
Gavia immer	Common Loon	b	B	b	B	B
Gavia adamsii	Yellow-billed Loon	w		w		
PODICIPEDIFORMES						
Podicipedidae						
Podilymbus podiceps	Pied-billed Grebe		i/c			
Podiceps auritus	Horned Grebe	b	B	w	(b)	B
Podiceps grisegena	Red-necked Grebe	B	(b)	w		B
Aechmophorus occidentalis	Western Grebe			i/c		
PROCELLARIIFORMES						
Diomedeidae						
Phoebastria nigripes	Black-footed Albatross			p		
Procellariidae						
Fulmarus glacialis	Northern Fulmar			p		
Puffinus carneipes	Flesh-footed Shearwater			p		
Puffinus griseus	Sooty Shearwater			p		
Puffinus tenuirostris	Short-tailed Shearwater			p		
Hydrobatidae						
Oceanodroma furcata	Fork-tailed Storm-Petrel			B		
Oceanodroma leucorhoa	Leach's Storm-Petrel			(b)		
PELECANIFORMES						
Phalacrocoracidae						
Phalacrocorax auritus	Double-crested Cormorant	b		(b)		i/c
Phalacrocorax pelagicus	Pelagic Cormorant	b		B		
CICONIIFORMES						
Ardeidae						
Botaurus lentiginosus	American Bittern			i/c		
Ardea herodias	Great Blue Heron	(b)		B	?	
Ardea alba	Great Egret			i/c		
Cathartidae						
Cathartes aura	Turkey Vulture					i/c
ANSERIFORMES						
Anatidae						
Anser albifrons	Great White-fronted Goose	m	m	m		m
Chen canagica	Emperor Goose			i/c		
Chen caerulescens	Snow Goose	m	m	m	m	i/c
Branta canadensis	Canada Goose	B	B	B	(b)	B
Branta bernicla	Brant	m		m		i/c
Cygnus buccinator	Trumpeter Swan	B	B	m	B	B
Cygnus columbianus	Tundra Swan	m	m	m		m
Anas strepera	Gadwall			w		(b)
Anas penelope	Eurasian Wigeon	i/c		i/c		
Anas americana	American Wigeon	B	(b)	(b)	B	B
Anas rubripes	American Black Duck			i/c		
Anas platyrhynchos	Mallard	B	B	B	b	B
Charadrius vociferus	Killdeer	(b)	(b)	b	?	(b)

		WRST	KNPR	GLBA	TAT	TLN
Anas discors	Blue-winged Teal	(b)	(b)	m	(b)	B
Anas cyanoptera	Cinnamon Teal		i/c	i/c	i/c	i/c
Anas clypeata	Northern Shoveler	b	b	b	(b)	B
Anas acuta	Northern Pintail	b	B	B	B	B
Anas crecca	Green-winged Teal	B	B	B	B	B
Aythya valisineria	Canvasback	(b)	(b)	m	B	B
Aythya americana	Redhead	(b)	i/c	i/c	(b)	(b)
Aythya collaris	Ring-necked Duck	b		m	?	B
Aythya marila	Greater Scaup	b	B	m	(b)	B
Aythya affinis	Lesser Scaup	b	B	B	B	B
Somateria spectabilis	King Eider			m		
Somateria mollissima	Common Eider			B		
Histrionicus histrionicus	Harlequin Duck	B	b	B	(b)	(b)
Melanitta perspicillata	Surf Scoter	b	B	w	(b)	B
Melanitta fusca	White-winged Scoter	b	B	w	b	B
Melanitta nigra	Black Scoter	?	m	w		
Clangula hyemalis	Long-tailed Duck	?	m	b	?	i/c
Bucephala albeola	Bufflehead	B	B	(b)	?	B
Bucephala clangula	Common Goldeneye	b	B	w	B	B
Bucephala islandica	Barrow's Goldeneye	B	B	B	b	B
Lophodytes cucullatus	Hooded Merganser			B	(b)	
Mergus merganser	Common Merganser	b	B	B	B	i/c
Mergus serrator	Red-breasted Merganser	B	b	B	(b)	i/c
Oxyura jamaicensis	Ruddy Duck		i/c			B
FALCONIFORMES						
Accipitridae						
Pandion haliaetus	Osprey		(b)	m	(b)	B
Haliaeetus leucocephalus	Bald Eagle	B	B	B	B	B
Circus cyaneus	Northern Harrier	b	b	m	(b)	(b)
Accipiter striatus	Sharp-shinned Hawk	B	B	B	B	B
Accipiter gentilis	Northern Goshawk	B	B	B	B	B
Buteo swainsoni	Swainson's Hawk	i/c	m	m		i/c
Buteo jamaicensis	Red-tailed Hawk	B	B	B	b	B
Buteo lagopus	Rough-legged Hawk	m	m	m	m	m
Aquila chrysaetos	Golden Eagle	B	B	(b)	B	B
Falconidae						
Falco sparverius	American Kestrel	(b)	B	m	b	B
Falco columbarius	Merlin	B	B	m	(b)	B
Falco rusticolus	Gyrfalcon	B	B		B	b
Falco peregrinus	Peregrine Falcon	(b)	B	B	(b)	B
GALLIFORMES						
Phasianidae						
Bonasa umbellus	Ruffed Grouse	(b)	B			B
Falcipennis canadensis	Spruce Grouse	B	B		B	B
Lagopus lagopus	Willow Ptarmigan	B	B	B	B	B
Lagopus mutus	Rock Ptarmigan	b	B	B	B	(b)
Lagopus leucurus	White-tailed Ptarmigan	(b)	B	B	B	(b)
Dendragapus obscurus	Blue Grouse			B	B	
Tympanuchus phasianellus	Sharp-tailed Grouse	b				B
GRUIFORMES						
Rallidae						
Porzana carolina	Sora				?	(b)
Fulica americana	American Coot	i/c	i/c	m		B
Gruidae						
Grus canadensis	Sandhill Crane	?	m	m	?	B
CHARADRIIFORMES						
Charadriidae						
Pluvialis squatarola	Black-bellied Plover			m		i/c
Pluvialis dominica	American Golden-Plover		B	m	?	B
Pluvialis fulva	Pacific Golden-Plover	m				
Charadrius semipalmatus	Semipalmated Plover	b	B	B	B	B

		WRST	KNPR	GLBA	TAT	TLN
Haematopodidae						
Haematopus bachmani	Black Oystercatcher	b		B		
Scolopacidae						
Tringa melanoleuca	Greater Yellowlegs	B	i/c	B	B	i/c
Tringa flavipes Lesser	Yellowlegs	b	B	B	B	B
Tringa solitaria	Solitary Sandpiper	B	(b)	B	(b)	B
Heteroscelus incanus	Wandering Tattler	(b)	b	(b)	B	(b)
Actitis macularia	Spotted Sandpiper	B	B	B	B	B
Bartramia longicauda	Upland Sandpiper	B	(b)	i/c	?	(b)
Numenius phaeopus	Whimbrel	(b)		m	?	B
Numenius tahitiensis	Bristle-thighed Curlew			i/c		
Limosa haemastica	Hudsonian Godwit			m	B	i/c
Limosa lapponica	Bar-tailed Godwit			i/c		
Limosa fedoa	Marbled Godwit			m		
Arenaria interpres	Ruddy Turnstone			m		i/c
Arenaria melanocephala	Black Turnstone	i/c		m		i/c
Aphriza virgata	Surfbird	B		m		i/c
Calidris canutus	Red Knot	i/c		m		
Calidris alba	Sanderling	w	m	w		
Calidris pusilla	Semipalmated Sandpiper	m	m	m	m	m
Calidris mauri	Western Sandpiper	m		m	m	m
Calidris ruficollis	Red-necked Stint			i/c		
Calidris minutilla	Least Sandpiper	b	B	B	B	(b)
Calidris bairdii	Baird's Sandpiper	m		m	m	m
Calidris melanotos	Pectoral Sandpiper	m	i/c	m	m	m
Calidris ptilocnemis	Rock Sandpiper			w		
Calidris alpina	Dunlin	i/c	i/c	m	m	
Tryngites subruficollis	Buff-breasted Sandpiper			i/c		i/c
Limnodromus griseus	Short-billed Dowitcher		(b)	m	B	i/c
Limnodromus scolopaceus	Long-billed Dowitcher	m		m	m	m
Gallinago gallinago	Common Snipe	B		B	B	B
Phalaropus lobatus	Red-necked Phalarope	b	B	(b)	B	B
Phalaropus fulicarius	Red Phalarope	i/c		i/c		
Laridae						
Stercorarius maccormicki	South Polar Skua			i/c		
Stercorarius pomarinus	Pomarine Jaeger	i/c		m		
Stercorarius parasiticus	Parasitic Jaeger	B		B		i/c
Stercorarius longicaudus	Long-tailed Jaeger	?	B	m		i/c
Larus ridibundus	Black-headed Gull					i/c
Larus philadelphia	Bonaparte's Gull	(b)	B	(b)	B	B
Larus canus	Mew Gull	B	B	B	B	B
Larus delawarensis	Ring-billed Gull	?				
Larus argentatus	Herring Gull	B	B	B	B	i/c
Larus thayeri	Thayer's Gull			b		
Larus glaucescens	Glaucous-winged Gull	b	i/c	B		i/c
Larus hyperboreus	Glaucous Gull			m	m	i/c
Xema sabini Sabine's	Gull	i/c		m		i/c
Rissa tridactyla	Black-legged Kittiwake	(b)		B	i/c	
Rhodostethia rosea	Ross's Gull			i/c		
Pagophila eburnea	Ivory Gull			i/c		
Sterna caspia	Caspian Tern			i/c		
Sterna hirundo	Common Tern			i/c		
Sterna paradisaea	Arctic Tern	B	B	B	B	B
Sterna aleutica	Aleutian Tern	(b)		B		
Chlidonias niger	Black Tern					i/c
Alcidae						
Uria aalge	Common Murre	(b)		B		
Cepphus columba	Pigeon Guillemot	(b)		B		
Brachyramphus marmoratus	Marbled Murrelet	b		b		
Brachyramphus brevirostris	Kittlitz's Murrelet	b		b		
Synthliboramphus antiquus	Ancient Murrelet	(b)		?		
Ptychoramphus aleuticus	Cassin's Auklet			m		
Aethia psittacula	Parakeet Auklet			i/c		

		WRST	KNPR	GLBA	TAT	TLN
Aethia cristatella	Crested Auklet	i/c				
Cerorhinca monocerata	Rhinoceros Auklet			m		
Fratercula corniculata	Horned Puffin			B		
Fratercula cirrhata	Tufted Puffin			B		
COLUMBIFORMES						
Columbidae						
Columba livia	Rock Dove				i/c	i/c
Columba fasciata	Band-tailed Pigeon			i/c		
Zenaida macroura	Mourning Dove	i/c	i/c	i/c		
STRIGIFORMES						
Strigidae						
Otus kennicottii	Western Screech-Owl			i/c		
Bubo virginianus	Great Horned Owl	B	B	(b)	(b)	B
Nyctea scandiaca	Snowy Owl	w	w	i/c	m	i/c
Surnia ulula	Northern Hawk Owl	B	B		B	B
Strix nebulosa	Great Gray Owl	(b)	(b)			B
Asio flammeus	Short-eared Owl	B	b	(b)	(b)	(b)
Aegolius funereus	Boreal Owl	b	b	i/c		B
Aegolius acadicus	Saw-whet Owl				?	
CAPRIMULGIFORMES						
Caprimulgidae						
Chordeiles minor	Common Nighthawk		b	i/c	(b)	i/c
APODIFORMES						
Apodidae						
Chaetura vauxi	Vaux's Swift			i/c	?	
Trochilidae						
Calypte anna	Anna's Hummingbird					i/c
Selasphorus rufus	Rufous Hummingbird	b	i/c	B	(b)	
CORACIIFORMES						
Alcedinidae						
Ceryle alcyon	Belted Kingfisher	B	(b)	B	B	B
PICIFORMES						
Picidae						
Sphyrapicus varius	Yellow-bellied Sapsucker				?	(b)
Sphyrapicus ruber	Red-breasted Sapsucker	i/c		i/c	B	i/c
Picoides pubescens	Downy Woodpecker	B	(b)	i/c	(b)	i/c
Picoides villosus	Hairy Woodpecker	B	(b)	b	B	b
Picoides tridactylus	Three-toed Woodpecker	B	B	B	(b)	b
Picoides arcticus	Black-backed Woodpecker	b	B		(b)	b
Colaptes auratus	Northern Flicker	B	B	B	B	B
PASSERIFORMES						
Tyrannidae						
Contopus cooperi	Olive-sided Flycatcher	(b)	b	(b)	(b)	(b)
Contopus sordidulus	Western Wood-Pewee	B	b	(b)	(b)	(b)
Empidonax flaviventris	Yellow-bellied Flycatcher					i/c
Empidonax alnorum	Alder Flycatcher	b	B	b	(b)	B
Empidonax minimus	Least Flycatcher		(b)		(b)	i/c
Empidonax hammondii	Hammond's Flycatcher	(b)	i/c	i/c	(b)	i/c
Empidonax oberholseri	Dusky Flycatcher		i/c			
Empidonax difficilis	Pacific-slope Flycatcher			b		
Sayornis phoebe	Eastern Phoebe		i/c			
Sayornis saya	Say's Phoebe	B	B	b	B	(b)
Tyrannus tyrannus	Eastern Kingbird		i/c	i/c		
Tyrannus forficatus	Scissor-tailed Flycatcher			i/c		
Laniidae						
Lanius excubitor	Northern Shrike	(b)	(b)	w	B	b
Vireonidae						
Vireo solitarius	Blue-headed Vireo		i/c			
Vireo gilvus	Warbling Vireo				?	i/c
Corvidae						
Perisoreus canadensis	Gray Jay	B	B	?	B	B

		WRST	KNPR	GLBA	TAT	TLN
Cyanocitta stelleri	Steller's Jay	i/c	(b)	B	(b)	
Nucifraga columbiana	Clark's Nutcracker		i/c	i/c		
Pica hudsonia	Black-billed Magpie	b	B	?	B	b
Corvus caurinus	Northwestern Crow		i/c	B		
Corvus corax	Common Raven	B	B	B	B	B
Alaudidae						
Eremophila alpestris	Horned Lark	b	B	m	B	(b)
Hirundinidae						
Tachycineta bicolor	Tree Swallow	B	B	B	B	B
Tachycineta thalassina	Violet-green Swallow	B	B	B	B	B
Stelgidopteryx serripennis	Northern Rough-winged Swallow			?		
Riparia riparia	Bank Swallow	B	B	B	B	B
Petrochelidon pyrrhonota	Cliff Swallow	B	B	m	B	B
Hirundo rustica	Barn Swallow	B	B	B	B	(b)
Paridae						
Poecile atricapillus	Black-capped Chickadee	b	b	i/c	B	B
Poecile gambeli	Mountain Chickadee		i/c			
Poecile rufescens	Chestnut-backed Chickadee	b		B	(b)	
Poecile hudsonica	Boreal Chickadee	B	B		B	B
Poecile cincta	Gray-headed Chickadee					i/c
Sittidae						
Sitta canadensis	Red-breasted Nuthatch	b	(b)	m	b	i/c
Certhiidae						
Certhia americana	Brown Creeper	(b)	i/c	b	?	i/c
Troglodytidae						
Troglodytes troglodytes	Winter Wren	(b)		B	b	
Cinclidae						
Cinclus mexicanus	American Dipper	B	b	B	(b)	b
Regulidae						
Regulus satrapa	Golden-crowned Kinglet	B	b	B	b	i/c
Regulus calendula	Ruby-crowned Kinglet	B	b	B	(b)	B
Sylviidae						
Phylloscopus borealis	Arctic Warbler	(b)				i/c
Turdidae						
Oenanthe oenanthe	Northern Wheatear	B	(b)			i/c
Sialia currucoides	Mountain Bluebird	B	B	i/c	(b)	(b)
Myadestes townsendi	Townsend's Solitaire	B	B	i/c	B	(b)
Catharus minimus	Gray-cheeked Thrush	b	B	B	B	(b)
Catharus ustulatus	Swainson's Thrush	B	B	B	B	B
Catharus guttatus	Hermit Thrush	b	B	B	B	B
Turdus migratorius	American Robin	B	B	B	B	B
Ixoreus naevius	Varied Thrush	B	B	b	B	B
Sturnidae						
Sturnus vulgaris	European Starling		B	?	(b)	(b)
Motacillidae						
Motacilla alba	White Wagtail			i/c		
Motacilla lugens	Black-backed Wagtail					i/c
Anthus rubescens	American Pipit	B	B	B	B	(b)
Bombycillidae						
Bombycilla garrulus	Bohemian Waxwing	B	B	i/c	B	B
Bombycilla cedrorum	Cedar Waxwing				?	
Parulidae						
Vermivora peregrina	Tennessee Warbler		B		(b)	i/c
Vermivora celata	Orange-crowned Warbler	B	B	B	(b)	B
Dendroica petechia	Yellow Warbler	(b)	B	B	b	(b)
Dendroica coronata	Yellow-rumped Warbler	B	B	B	b	B
Dendroica townsendi	Townsend's Warbler	B		b	(b)	(b)
Dendroica palmarum	Palm Warbler		i/c			
Dendroica striata	Blackpoll Warbler	(b)	B	i/c	(b)	m
Setophaga ruticilla	American Redstart		B	i/c	B	
Seiurus noveboracensis	Northern Waterthrush	b	b		(b)	B
Oporornis tolmiei	MacGillivray's Warbler		(b)	i/c	(b)	

		WRST	KNPR	GLBA	TAT	TLN
Geothlypis trichas	Common Yellowthroat		(b)	B	(b)	i/c
Wilsonia pusilla	Wilson's Warbler	b	B	B	B	(b)
Thraupidae						
Piranga ludoviciana	Western Tanager		i/c	i/c		
Emberizidae						
Spizella arborea	American Tree Sparrow	B	B	m	B	B
Spizella passerina	Chipping Sparrow		B	i/c	(b)	B
Spizella pallida	Clay-colored Sparrow					i/c
Spizella breweri	Brewer's Sparrow	B	B		B	(b)
Chondestes grammacus	Lark Sparrow					i/c
Passerculus sandwichensis	Savannah Sparrow	B	B	B	b	B
Passerella iliaca	Fox Sparrow	b	B	B	b	B
Melospiza melodia	Song Sparrow	b	B	B	b	i/c
Melospiza lincolnii	Lincoln's Sparrow	B	B	B	(b)	B
Zonotrichia albicollis	White-throated Sparrow		i/c			i/c
Zonotrichia leucophrys	White-crowned Sparrow	B	B	m	b	B
Zonotrichia atricapilla	Golden-crowned Sparrow	b	B	B	B	i/c
Junco hyemalis	Dark-eyed Junco	B	B	B	b	B
Calcarius lapponicus	Lapland Longspur	b	m	m		m
Calcarius pictus	Smith's Longspur	B	(b)	i/c		(b)
Plectrophenax nivalis	Snow Bunting	b	B	B	B	m
Icteridae						
Agelaius phoeniceus	Red-winged Blackbird	(b)	B	B	(b)	B
Sturnella neglecta	Western Meadowlark					i/c
Euphagus carolinus	Rusty Blackbird	b	B	B	(b)	B
Molothrus ater	Brown-headed Cowbird	i/c	i/c	i/c	i/c	i/c
Fringillidae						
Fringilla montifringilla	Brambling	i/c				
Leucosticte tephrocotis	Gray-crowned Rosy-Finch	(b)	B	B	(b)	i/c
Pinicola enucleator	Pine Grosbeak	(b)	(b)	B	b	b
Carpodacus purpureus	Purple Finch		i/c			i/c
Loxia curvirostra	Red Crossbill	(b)	B	w		
Loxia leucoptera	White-winged Crossbill	b	B	w	b	B
Carduelis flammea	Common Redpoll	B	B	B	B	b
Carduelis hornemanni	Hoary Redpoll	w		i/c		w
Carduelis pinus	Pine Siskin	b	B	B	b	i/c

APPENDIX B. Checklist of mammals observed in the four St. Elias Mountain parks and Tetlin Wildlife Refuge.

WRST	Wrangell-St. Elias National Park and Preserve	D	Definitely occurs within park/refuge boundaries
KNPR	Kluane National Park	L	Likely occurs within boundaries
GLBA	Glacier Bay National Park and Preserve	P	Possibly occurs within boundaries
TAT	Tatshenshini-Alsek Provincial Park	X	Extirpated
TLN	Tetlin National Wildlife Refuge	*	Incidental occurrence

		WRST	KNPR	GLBA	TAT	TLN
INSECTIVORA						
Soricidae						
Sorex cinereus	Cinereus/Masked Shrew	D	D	D	D	D
Sorex hoyi	Pygmy Shrew	D	L	P	D	
Sorex monticolus	Montane/Dusky Shrew	D	D	D	D	D
Sorex palustris	American Water Shrew	D	L	D	D	P
Sorex tundrensis	Tundra Shrew	D			D	P
Sorex yukonicus	Tiny Shrew	D				P
CHIROPTERA						
Vespertilionidae						
Myotis lucifugus	Little Brown Bat	D	D	D	L	D
LAGOMORPHA						
Ochotonidae						
Ochotona collaris	Collared Pika	D	D		D	P
Leporidae						
Lepus americanus	Snowshoe Hare	D	D	D	D	D
RODENTIA						
Sciuridae						
Tamias minimus	Least Chipmunk		D		D	
Marmota monax	Woodchuck		D*			
Marmota broweri	Alaskan Marmot					
Marmota caligata	Hoary Marmot	D	D	D	D	P
Spermophilus parryii	Arctic Ground Squirrel	D	D		D	L
Tamiasciurus hudsonicus	American Red Squirrel	D	D	D	D	D
Glaucomys sabrinus	Northern Flying Squirrel	L	D	D	L	D
Castoridae						
Castor canadensis	American Beaver	D	D	D	D	D
Muridae						
Peromyscus maniculatus	Deer Mouse		D		D	
Peromyscus keeni	Northwestern Deer Mouse			D		
Neotoma cinerea	Bushy-tailed Woodrat		L		D	
Clethrionomys rutilus	Northern Red-Backed Vole	D	D	D	D	D
Phenacomys ungava	Eastern Heather Vole		D			
Microtus longicaudus	Long-tailed Vole	D	D	D	D	P
Microtus miurus	Singing/Insular Vole	D	D			P
Microtus oeconomus	Northern/Tundra Vole	D	D	D	D	L
Microtus pennsylvanicus	Meadow Vole	D	D			D
Microtus xanthognathus	Taiga/Chestnut-cheeked Vole	L				D
Ondatra zibethicus	Muskrat	D	L		D	D
Lemmus sibiricus	Brown/Siberian Lemming	D	L		P	L
Synaptomys borealis	Northern Bog Lemming	D	D		L	D
Dipodidae						
Zapus hudsonius	Meadow Jumping Mouse	L	D		D	
Erethizontidae						
Erethizon dorsatum	American Porcupine	D	D	D	D	D
CARNIVORA						
Canidae						
Canis latrans	Coyote	D	D	D	D	D
Canis lupus	Wolf	D	D	D	D	D
Vulpes vulpes	Red Fox	D	D	D	D	D

		WRST	KNPR	GLBA	TAT	TLN
Ursidae						
Ursus americanus	American Black Bear	D	D	D	D	D
Ursus arctos	Grizzly Bear	D	D	D	D	D
Mustelidae						
Martes americana	American Marten	D	D	D	D	D
Mustela erminea	Ermine	L	D	D	L	D
Mustela nivalis	Least Weasel	P	D	D	P	D
Mustela vison	American Mink	D	D	D	L	D
Gulo gulo	Wolverine	D	D	D	D	D
Lutra canadensis	River Otter	L	D	D	D	D
Felidae						
Felis concolor	Cougar		D*			
Lynx lynx	Lynx	D	D	D	D	D
ARTIODACTYLA						
Cervidae						
Rangifer tarandus	Caribou	D	D		X	D
Odocoileus hemionus	Mule Deer		D	D		
Alces alces	Moose	D	D	D	D	D
Bovidae						
Bison bison	American Bison	D				D*
Oreamnos americanus	Mountain Goat	D	D	D	D	
Ovis dalli	Dall Sheep	D	D		D	D

Distribution of, and Microhabitat Use by, Woodland Salamanders Along Forest-Farmland Edges

GRETCHEN I. YOUNG[1,2] and RICHARD H. YAHNER[1]

[1]School of Forest Resources, 107 Ferguson Building, Pennsylvania State University, University Park, Pennsylvania 16802 U.S.A.
[2]185 Massa Drive, Windsor, Pennsylvania 17366 U.S.A.

Young, Gretchen I., and Richard H. Yahner. 2003. Distribution of, and microhabitat use by, woodland salamanders along forest-farmland edges. Canadian Field-Naturalist 117(1): 19–24.

We examined the distribution of, and microhabitat use by, woodland salamander populations along forest-farmland edges at six sites (each 40 ha) in the Valley and Ridge Province of Pennsylvania (U.S.A.) from September to November 1995 and from March to May 1996. We found 570 salamanders of nine species, with most (90.5%) being Redback Salamanders (*Plethodon cinereus*). Observed versus expected numbers of salamanders of all species combined differed with distances from edges ($P < 0.005$); only 64 (11%) were found at the immediate edge (i.e., 5 m into the forest at the forest-farmland edge). This finding is partially related to dryer microclimatic conditions at edges. Two of the sites (BL2 and SH1) with the highest number of Redback Salamanders contained higher density of logs, soil temperatures, and percentage coverage of herbaceous growth in fall, and deeper and higher percentage coverage of leaf litter in spring compared to other sites. Woodland salamanders and other amphibians are of conservation concern because of regional population declines and range reductions. Thus, we recommend that cool, moist microclimatic conditions be preserved along forest-farmland edges (e.g., via retention of shaded logs and spring seeps) whenever possible for the conservation of woodland salamander populations.

Key Words: edge, farmland, forest, microhabitat, Redback Salamander, *Plethodon cinereus,* woodland salamanders, Pennsylvania.

Habitat loss, forest management, acid deposition, and other environmental perturbations have contributed to dramatic declines in regional and localized amphibian populations over the past few decades (Vitt et al. 1990; Blaustein 1994; Rodewald and Yahner 1999). Habitat loss created by timber harvesting, urbanization, or road construction can result in an increase in extent of edges (Yahner 2000). Microhabitat conditions; e.g., wind and solar radiation patterns, along edges of forest stands often are much different than conditions within forest interiors (Ranney et al. 1981; Franklin and Forman 1987). These drier conditions can have negative impacts on amphibian populations (Feder 1983; Rodewald and Yahner 1999).

Forest-farmland edges are extensive in the Valley and Ridge Province of Pennsylvania; valleys are intensively farmed, whereas ridges are forested (Geer 1997). The objective of our study was to determine the distribution of and microhabitat use by woodland salamanders along forest-farmland edges in the Valley and Ridge Province of Pennsylvania.

Study Area and Methods

We selected six 40-ha study sites in a four-county area of the Valley and Ridge Province of Pennsylvania, including one in Centre County, two in Juniata County, two in Perry County, and one in Cumberland County (details of sites are given in Geer 1997; site names and specific locations are in Table 2). Elevations of sites ranged from 630 to 1300 m. Four sites were arbitrarily located on north-facing slopes, and two were on south-facing slopes. Major tree taxa were pine (*Pinus* spp.), oak (*Quercus* spp.), hickory (*Carya* spp.), and black cherry (*Prunus serotina*).

We established five permanent transects per study site. Transects began at the forest-farmland edge (5 m into the forest) and extended 200 m into the forest perpendicular to the edge (i.e., towards the ridgeline). They were spaced 100 m apart. Five, 5-m radius plots were placed along each transect (i.e., 5, 50, 100, 150, and 200 m from the edge), giving 25 plots per study site.

Woodland salamanders were sampled once per season in fall (12 September and 9 November 1995) and again in spring (26 March to 22 May 1996) at each of the six study sites. At each 5-m radius plot, all rocks and logs were turned and checked for salamanders between early morning and early afternoon (0800 to 1300 hr); rocks and logs then were returned to original positions.

Observed versus expected numbers of salamanders were compared among the five distances from edges, using a *G*-test for goodness-of-fit (Sokal and Rohlf 1995). The observed numbers were based on data obtained at all sites and both seasons combined. The expected number of salamanders was calculated as the total number of observed salamanders divided by 5. The number of salamanders per distance from edges then was compared *a posteriori* about the cell (distance) of interest using *G*-tests for goodness-of-fit.

We measured 22 habitat variables during fall 1995 and spring 1996 at each plot (Table 1). These variables were selected because of potential biological relevance to the distribution of and microhabitat use by woodland salamanders (e.g., Heatwole 1962a, 1962b; Jaeger 1980; Rodewald and Yahner 1999).

Simple correlation analyses were used to determine associations between the 22 habitat variables and six salamander variables (Sokal and Rohlf 1995). The six salamander variables were mean number of Redback Salamanders at each site in fall and in spring, mean number of all other species of salamander species (excluding Redbacks) in fall and in spring, and mean species richness in fall and in spring.

Results

We found 570 salamanders of nine species during fall and spring along forest-farmland interfaces at the six study sites (Table 2). Of this total, 516 (90.5%) were Redback Salamanders, 19 (3.3%) Slimy Salamanders (*Plethodon glutinosus*), 16 (2.8%) Jefferson Salamanders (*Ambystoma jeffersonianum*), 11 (1.9%) Mountain Dusky Salamanders (*Desmognathus ochrophaeus*), two (0.4%) Valley and Ridge Salamanders (*Plethodon hoffmani*), two (0.4%) Northern Dusky Salamanders (*Desmognathus fuscus*), two (0.4%) Red-spotted Newts (red-eft phase, *Notophthalmus viridescens*), one (0.2%) Four-toed Salamander (*Hemidactylium scutatum*), and one (0.2%) Northern Red Salamander (*Pseudotriton ruber*).

Of the total number of salamanders, most (59%, $n = 338$) were observed in fall (Table 2). Moreover, the number of salamanders observed per site in both seasons combined varied from 164 (28%, site SH1) to 27 (5%, site RS1).

Observed versus expected numbers of salamanders differed with distances from edges in both fall

TABLE 1. Twenty-two microhabitat variables measured at 25 5-m radius plots at each of six study sites (forest-farmland edges) in Pennsylvania during fall 1995 and spring 1996. Sampling methods and procedures modified from James and Shugart (1970) and Yahner (1987).

Variable	Description and Sampling method
Number of logs	Number of fallen logs ≥ 1 m long ≥ 7.5 cm in diameter counted in a 5-m radius circle centered on a plot.
Number of stumps	Number of dead trees ≤ 1.5 m tall, ≥ 7.5 cm in diameter counted in a 5-m radius circle centered on a plot.
Number of short shrubs	Number of shrubs 0.5-1.4 m tall and ≤ 2.5 cm in diameter by genus 1 m to the right of north-south and east-west transects that run the length of the 5-m radius circle plot.
Number of tall shrubs	Number of shrubs ≥ 1.5 m tall and ≤ 2.5 cm in diameter by genus 1 m to the right of north-south and east-west transects that run the length of the 5-m radius circle plot.
Number of understory trees	Number of trees ≥ 1.5 m tall and 2.5-7.5 cm dbh (diameter at breast height) by genus 1 m to the right of perpendicular north-south and east-west transects in a 5-m radius circle plot.
Percentage log cover	Number of 1-m intervals in each north-south and east-west transect in which the cross hairs of the ocular tube fall on fallen logs at ground level (× 100%).
Percentage herbaceous cover	Number of 1-m intervals in each north-south and east-west transect in which the cross hairs of the ocular tube intercept herbaceous vegetation at ground level (× 100%)
Percentage leaf litter cover	Number of 1-m intervals in each north-south and east-west transect in which the cross hairs of the ocular tube intercept leaf litter at ground level (× 100%).
Percentage rock cover	Number of 1-m intervals in each north-south and east-west transect in which the cross hairs of the ocular tube intercept rock at ground level (× 100%).
Percentage bare ground cover	Number of 1-m intervals in each north-south and east-west transect in which the cross hairs of the ocular tube intercept bare ground at ground level (× 100%).
Percentage canopy cover	Number of 1-m intervals in each north-south and east-west transect in which the cross hairs of the ocular tube intercept canopy, when held above the head (× 100%).
Number of overstory trees	Total number of overstory trees ≥ 1.5 m tall and ≥ 7.5 cm dbh by tree genus in a 5-m radius circle plot.

TABLE 1. (Continued)

Variable	Description and Sampling method
Basal area of overstory trees	Basal area (m^2/ha) of total number of overstory trees defined and measured as described above.
Elevation	Elevation (m) above sea level at center of site from U. S. Geological Survey topographic map.
Aspect	Compass direction (degrees) measured along gradient of slope at center of site (if slope ≥ 10°).
Distance to edge	Distance to edge (0-200 m) created by agriculture (e.g., pasture).
Distance to standing water	Measurement (<25, 25-50, >50 m) to a spring seep or vernal pool.
Distance to running water	Measurement (<25, 25-50, >50 m) to a woodland stream or spring.
Soil temperature	Temperature (°C) measured at the center of the 5-m radius circle plot with a Reotemp bimetal Thermometer.
Soil moisture	Soil moisture content measured at the center of the 5-m radius circle plot with a Kelway Soil Acidity and Moisture Tester.
Soil pH	Soil acidity (pH) measured at the center of the 5-m radius circle plot with a Kelway Soil Acidity and Moisture Tester.
Leaf litter depth	Leaf litter measured in cm at the four cardinal directions at each of the 5-m radius circle plots.

and spring combined ($G = 41.4$, $P < 0.005$) (Table 3). Only 64 (11%) of these were found directly at the edge (5 m into the forest); this finding was significantly lower than expected ($G = 31.4$, $P < 0.0005$).

In contrast, the observed number of salamanders was considerably higher at other distances from the edge, ranging from 103 (18%) at 50 m to 149 (26%) at 100 m from the edge.

Mean numbers of Redback Salamanders were positively correlated with number of stumps in fall and spring, percentage leaf litter in fall, and leaf litter depth and percentage canopy cover in spring (Table 4). Mean numbers of all other salamander species combined were positively correlated with percentage leaf litter in fall and with leaf litter depth, number of short shrubs, and percentage canopy cover in spring. Species richness of all species combined was negatively correlated with soil pH and positively correlated with percentage rock cover in both seasons. Of the six salamander variables, only species richness of all species was correlated with distance to edge, with a negative correlation noted in fall.

Discussion

Our study has shown that the abundance of woodland salamander populations was lower immediately along forest-farmland edges compared to distances farther from edges. This finding is similar to results reported along edges created by timbering-harvesting practices (deMaynadier and Hunter 1998). Forest edges have lower humidity and higher air temperatures, higher soil temperatures, increased solar radiation, and lower soil moisture relative to forested areas away from edges (e.g., Ranney et al. 1981; Brothers and Spingarn 1992). Hence, microhabitat conditions created along forest edges (e.g., increased soil temperture or reduced soil moisture) are generally unfavorable for woodland salamanders (Petranka et al. 1993; deMaynadier and Hunter 1998; Rodewald and Yahner 1999; Yahner et al. 2001a).

Aspect of forest-farmland edges can affect woodland salamander populations because south-facing slopes tend to be warmer and dryer than north-facing slopes (Collier et al. 1973); however, aspect did not affect salamander populations in this study (see Geer 1997). Furthermore, lower numbers of salamanders along edges may be related to other factors, such as greater abundance of predators along forest edges than in forest interiors (e.g., Bollinger and Peak 1995; Fenske-Crawford and Niemi 1997; but see Yahner et al. 2001b). However, predator abundance was not measured in our study.

We recommend that cool, moist microclimatic conditions be preserved whenever possible for the benefit of woodland salamanders. This can be accomplished by the retention of forest floor cover objects (i.e., shaded rocks and stumps); the preservation of moist environments, especially those associated with spring seeps; and the retention of understory vegetation as a source of shade along forest edges. Rodewald and Yahner (1999), for instance, noted that abundance of several woodland salamander species was positively associated with soil moisture, percentage coverage of rocks, and

TABLE 2. Species richness and number of individuals per terrestrial salamander species under natural substrates at six study sites (forest-farmland edges) in Pennsylvania during fall 1995 and spring 1996.

	Fall 1995						pring 1996						
Salamander Variable	RS1[1]	SH1[1]	SH2[1]	BL1[1]	BL2[1]	MHS1[1]	RS1[1]	SH1[1]	SH2[1]	BL1[1]	BL2[1]	MHS1[1]	Total
Species Richness	3	3	3	4	3	2	4	3	4	7	4	3	9
Number of Individuals:													
Redback Salamander *(Plethodon cinereus)*	1	60	21	17	75	38	1	99	42	55	63	44	516
Slimy Salamander *(Plethodon glutinosus)*	3	4	1	2	3	0	0	1	1	1	3	0	19
Jefferson Salamander *(Ambystoma jeffersoniarum)*	6	0	0	0	0	0	9	0	0	1	0	0	16
Northern Dusky Salamander *(Desmognathus fuscus)*	0	0	0	1	0	0	0	0	0	1	0	0	2
Mountain Dusky Salamander *(Desmognathus ochrophaeus)*	0	0	0	0	0	0	6	0	0	5	0	0	11
Red-spotted Newt (red eft) *(Notophthalmus viridescens)*	0	0	0	0	0	0	0	0	0	1	0	1	2
Four-toed Salamander *(Hemidactylium scutatum)*	0	0	0	0	0	0	1	0	0	0	0	0	1
Valley and Ridge Salamander *(Plethodon hoffmani)*	0	0	0	0	0	0	0	0	2	0	0	0	2
Northern Red Salamander *(Pseudotriton ruber)*	0	0	0	0	0	0	0	0	0	0	1	0	1
TOTAL	10	64	22	20	78	38	17	100	45	64	67	45	570

[1] RS1= Rock Springs (40°42'20", 77°58'00"), SH1=Spruce Hill 1 (40°26'40", 77°28'00"), SH2=Spruce Hill 2 (40°27'30", 77°27'30"), BL1=Blain 1 (40°21'00", 77°31'30"), BL2=Blain 2 (40°19'50", 77°33'00"), MHS1=Mount Holly Springs (40°06'30", 77°16'00").

TABLE 3. Distribution of woodland salamanders along transects at six study sites (forest-farmland edges) in Pennsylvania during fall 1995 and spring 1996.

	Distance from edge (m)				
Season	0	50	100	150	200
Fall 1995:					
Redback Salamander	22	40	55	50	45
Slimy Salamander	0	0	5	3	5
Jefferson Salamander	0	0	6	0	0
Northern Dusky Salamander	0	1	0	0	0
Mountain Dusky Salamander	0	0	0	0	0
Red-spotted Newt (red-eft)	0	0	0	0	0
Four-toed Salamander	0	0	0	0	0
Valley and Ridge Salamander	0	0	0	0	0
Northern Red Salamander	0	0	0	0	0
Spring 1996:	0	0	0	0	0
Redback Salamander	41	57	63	77	66
Slimy Salamander	0	1	0	5	0
Jefferson Salamander	0	0	10	0	0
Northern Dusky Salamander	0	0	1	0	0
Mountain Dusky Salamander	0	4	7	0	0
Red-spotted Newt (red-eft)	1	0	0	1	0
Four-toed Salamander	0	0	1	0	0
Valley and Ridge Salamander	0	0	1	0	1
Northern Red Salamander	0	0	0	1	0
Total	64	103	149	137	117

TABLE 4. Significant correlations ($P \leq 0.05$) between salamander variables and microhabitat variables measured at six study sites (forest-farmland edges) in Pennsylvania.

Microhabitat variable	RBS-F[1]	RBS-S[1]	ALL-F[1]	ALL-S[1]	SR-F[1]	SR-S[1]
Soil pH					-0.854	-0.975[2]
Soil moisture						0.849[2]
Leaf litter depth		0.855[2]		0.903[2]		
Distance to edge					-0.821[2]	
Number of short shrubs				0.770[2]		
Number of stumps	0.768[2]	0.814[2]				
% Leaf cover (fall)	0.903[2]		0.928[2]			
% Rock cover (fall)					0.925	0.943
% Rock cover (spring)					0.932	0.951
% Bare ground (spring)						0.837[2]
% Canopy cover (spring)		0.780[2]		0.790[2]		

[1]RBS-F = mean number of Redback Salamanders in fall, RBS-S = mean number of Redback Salamanders in spring, ALL-F = mean number of all other species of salamanders in fall, ALL-S = mean number of all other species of salamanders in spring, SR-F = species richness in fall, SR-S = species richness in spring. Microhabitat variables are described in Table 1.
[2]Salamander variable or microhabitat variable was log transformed.

percentage coverage of low-lying vegetation in mature forest stands. Thompson et al. (1980) found that Jefferson Salamanders occurred more often along forest edges characterized by a dense border of shrubs.

In conclusion, because many amphibian species are exhibiting worldwide declines in abundance and distribution (e.g., Blaustein 1994), we suggest that additional research be focused on the impacts of human-created edges on the natural history and behavior of woodland salamanders. As forests become increasingly fragmented by agricultural and timber-harvesting practices, the long-term perpetuation of woodland salamander populations will continue to be an important conservation issue.

Acknowledgments

We thank P. Ferreri, J. Lynch, and J. Pechmann for comments on an earlier draft of this manuscript, K. Derge for field assistance, and E. Hill for clerical assistance. This study was funded by the Pennsylvania Agricultural Experiment Station and the Max McGraw Wildlife Foundation.

Literature Cited

Blaustein, A. R. 1994. Chicken little or Nero's fiddle? A perspective on declining amphibian populations. Herpetologica 50: 85–97.

Bollinger, E. K., and **R. G. Peak.** 1995. Depredation of artificial avian nests: a comparison of forest-field and forest-lake edges. American Midland Naturalist 134: 200–203.

Brothers, T. S., and **A. Spingarn**. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology 6: 91–100.

Collier, B. D., G. W. Cox, A. W. Johnson, and **P. C. Miller.** 1973. Dynamic ecology. Prentice-Hall, Englewoods Cliff, New Jersey. 563 pages.

deMaynadier, P. G., and **M. L. Hunter, Jr.** 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology 12: 340–352.

Feder, M. E. 1983. Integrating the ecology and physiology of plethodontid salamanders. Herpetologica 39: 291–310.

Fenske-Crawford, T. J., and **G. J. Niemi.** 1997. Predaton of artificial ground nests at two types of edges in a forest-dominated landscape. Condor 99: 14–24.

Franklin, J. F., and **R. T. T. Forman**. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology 1: 5–18.

Geer, G. I. 1997. Terrestrial salamanders at forest-farmlands interfaces of Pennsylvania: relative abundance, distribution, and microhabitat use. M.S. thesis, Pennsylvania State University, University Park, Pennsylvania. 61 pages.

Petranka, J. W., M. E. Eldridge, and **K. E. Haley.** 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology 7: 363–370.

Ranney, J. W., M. C. Bruner, and **J. B. Levenson.** 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67-95 *in* Forest Island Dynamics in Man-Dominated Landscapes. *Edited by* R. L. Burgess and D. M. Sharpe. Springer-Verlag, New York, New York.

Rodewald, A. D., and **R. H. Yahner.** 1999. Effects of forest management and landscape composition on woodland salamanders. Northeast Wildlife 54: 45–54.

Sokal, R. R., and **F. J. Rohlf.** 1995. Biometry. 3rd edition. W. H. Freeman and Company, San Francisco, California. 859 pages.

Thompson, E. L., J. E. Gates, and **G. J. Taylor.** 1980. Distribution and breeding habitat selection of the Jefferson Salamander, *Ambystoma jeffersonianum*, in Maryland. Journal of Herpetology 14: 113–120.

Vitt, L. J., J. P. Caldwell, H. M. Wilbur, and **D. C. Smith.** 1990. Amphibians as harbingers of decay. BioScience 40: 418.

Yahner, R. H. 2000. Eastern Deciduous Forest: Ecology and Wildlife Conservation. 2nd edition. University of Minnesota Press, Minneapolis. 295 pages.

Yahner, R. H., W. C. Bramble, and **W. R. Byrnes.** 2001a. Effect of vegetation maintenance of an electric transmission right-of-way on reptile and amphibian populations. Journal of Arboriculture 27: 24–28.

Yahner, R. H., A. D. Rodewald, and **S. C. Talbott.** 2001b. Edge-related nest predation associated with the retention of residual trees in harvested hardwood stands. Canadian Field-Naturalist 115: 82-87.

Received 26 May 2000
Accepted 22 May 2003

Distribution, Abundance, and Status of the Greater Sage-Grouse, *Centrocercus urophasianus*, in Canada

CAMERON L. ALDRIDGE[1,2] and R. MARK BRIGHAM

Department of Biology, University of Regina, Regina, Saskatchewan S4S 0A2 Canada
[1]Corresponding Author's e-mail: aldridge@ualberta.ca
[2]Current Address: Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9 Canada

Aldridge, Cameron L., and R. Mark Brigham. 2003 Distribution, abundance, and status of the Greater Sage-Grouse, *Centrocercus urophasianus*, in Canada. Canadian Field-Naturalist 117(1): 25–34.

We reviewed the historic and present distribution of Greater Sage-Grouse (*Centrocercus urophasianus*) in Canada and found that the species has been eliminated from approximately 90% of its estimated historic distribution. Sage-grouse have been extirpated from British Columbia and reduced to remnant populations in Alberta and Saskatchewan. Estimates of the size of the population decline in Canada range from 66 to 92% over the last 30 years based on currently occupied habitat. As a result, sage grouse have been listed as Endangered in both Alberta and Saskatchewan by provincial governments and federally in Canada by COSEWIC. Intensive surveys from 1994 to 1999 in both provinces suggest that the 1999 spring breeding population had declined to between 813 and 1204 individuals. The number of active lek sites has continued to decline, suggesting that some habitats have become unsuitable to support viable sage-grouse populations. Number of yearling males recruiting to leks each spring has been low, suggesting that production and overwinter survival of young are the major problems related to the decline. Low chick survival rate, with only 18% surviving to 50 days of age, is the most likely parameter contributing to the population decline. These declines could be related to one or any combination of habitat changes, livestock grazing pressure, oil and gas developments, or climate change, all of which could lead to increased predation rates and decreased survival. It is questionable if the present population of sage-grouse in Canada is large enough to remain viable.

Key Words: Greater Sage-Grouse, *Centrocercus urophasianus*, distribution, endangered status, Saskatchewan, Alberta, Canada.

Sage-Grouse (*Centrocercus* spp.) are strongly associated with sagebrush (*Artemisia* spp.) habitats throughout the Great Plains and Intermountain West. Historically, they occurred in British Columbia, Alberta, Saskatchewan, and at least 16 U.S. states, but have been extirpated from British Columbia and five states (Braun 1998; Schroeder et al. 1999). The long-term decline in sage-grouse populations across their range was originally due to the direct loss of sagebrush steppe. This habitat has been reduced by more than 50% (2.5 million ha) since the early 1900s (Patterson 1952; Eng and Schladweiler 1972; Braun 1995).

Both Alberta and Saskatchewan still support Greater Sage-Grouse (*C. urophasianus*) populations, yet springtime lek counts indicate the Canadian population has decreased by approximately 80% since the mid-1980s to between 549 and 813 individuals in 1997 (Aldridge 1998). As a consequence of the decline, Alberta closed the Greater Sage-Grouse hunting season in 1996 for the first time since 1967 (Aldridge 1998). Greater Sage-Grouse have not been hunted in Saskatchewan since 1938 (Kerwin 1971).

In 1997, the Committee On the Status of Endangered Wildlife In Canada (COSEWIC) listed Greater Sage-Grouse as a Threatened species. This listing was upgraded to Endangered in 1998, reflecting the imminent threat of extinction in Canada (Hyslop 1998*).

Sage-grouse are found almost exclusively within the North American range of sagebrush and are associated with sagebrush habitats throughout the year (Patterson 1952; Braun et al. 1977; Connelly et al. 2000). This is also true in Canada, where Greater Sage-Grouse are found within the range of sagebrush in the semi-arid mixed-grass prairie. Silver Sage (*A. cana*) is the dominant species of sagebrush on the Canadian prairies and pasture sage (*Artemisia frigida*) is the main forb (Aldridge and Brigham 2002). Grasses commonly found include June Grass (*Koeleria macrantha*), Blue Grama (*Bouteloua gracilis*), Needle and Thread (*Stipa comata*), and Western Wheatgrass (*Agropyron smithii*) (Aldridge and Brigham 2002). Mean annual precipitation within the Alberta range is about 332 mm, and mean temperatures for July and January average 19.5 and -11.7°C, respectively (Onefour Research Station, Environment Canada).

Although sage-grouse have a close association with sagebrush habitats, specific habitat requirements vary throughout the year. Areas used by sage-grouse must contain suitable habitat which satisfies requirements for strutting grounds (leks), nesting areas, feeding and loafing sites, brood-rearing sites, and wintering areas (Klebenow 1969; Eng and Schladweiler 1972; Beck 1977).

*See Documents Cited section

Here we evaluate the distribution, abundance, status and viability of Greater Sage-Grouse in Canada and review potential factors that might be affecting the population. We also discuss long-term and present population trends, the apparent population decline, and range contraction, and we highlight recent research.

Distribution

Sage-grouse have been extirpated from at least five U. S. states (Arizona, Kansas, Nebraska, New Mexico, and Oklahoma) and one Canadian province, British Columbia (Braun 1998; Schroeder et al. 1999) (Figure 1). Throughout their range, sage-grouse have declined by 45-80% since the 1950s (Braun 1998). The long-term decline was originally due to the direct loss of sagebrush steppe (Patterson 1952; Braun 1995, 1998; Schroeder et al. 1999). Sage-grouse currently inhabit about 50% of the area they once occupied in Oregon (Crawford and Lutz 1985) and Colorado (Braun 1995) at the turn of the 20th century. Range contractions of similar magnitude have occurred throughout the species' range (Crawford and Lutz 1985; Swenson et al. 1987; Braun 1995). The current distribution of sage-grouse is highly fragmented (Eng and Schladweiler 1972; Hupp and Braun 1991; Braun 1995) (Figure 1).

At the northern edge of its range, Greater Sage-Grouse historically occurred in Canada (Figure 1), extending into the southern Okanagan and Similkameen valleys of British Columbia and across southeastern Alberta and southwestern Saskatchewan. The species was considered extirpated from British Columbia by 1918 (Cannings et al. 1987). Historically, Greater Sage-Grouse occupied approximately 100 000 km^2 within Alberta and

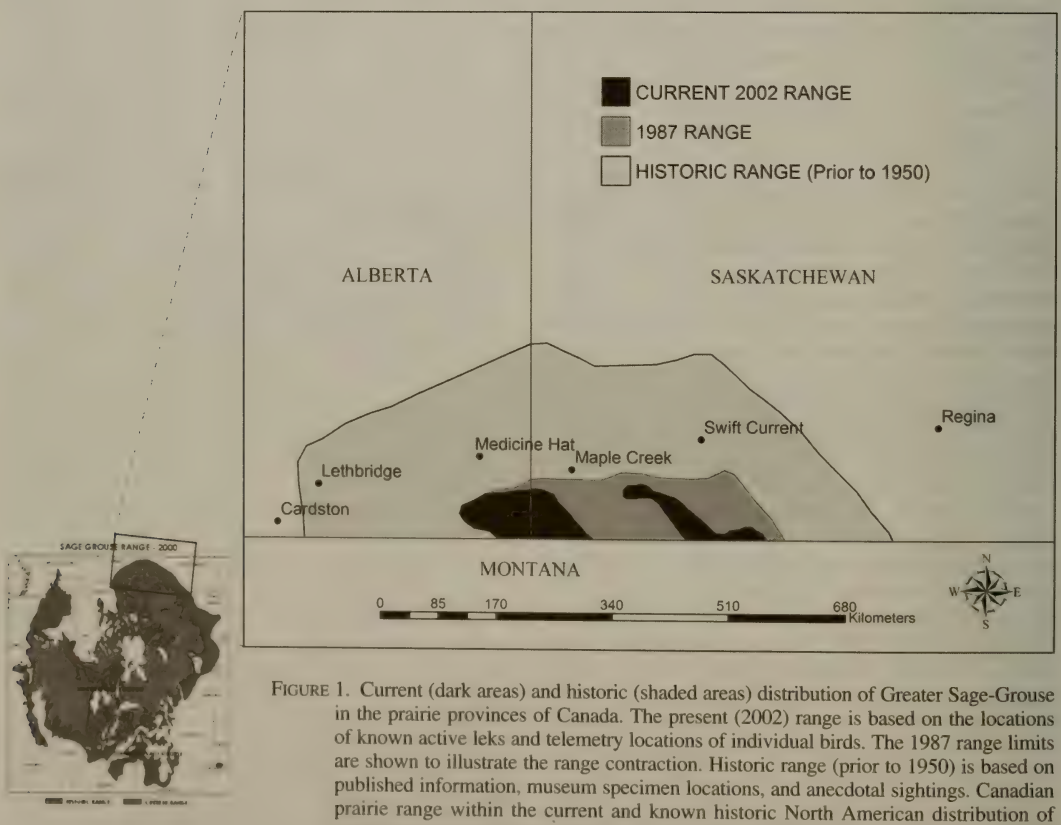


FIGURE 1. Current (dark areas) and historic (shaded areas) distribution of Greater Sage-Grouse in the prairie provinces of Canada. The present (2002) range is based on the locations of known active leks and telemetry locations of individual birds. The 1987 range limits are shown to illustrate the range contraction. Historic range (prior to 1950) is based on published information, museum specimen locations, and anecdotal sightings. Canadian prairie range within the current and known historic North American distribution of sage-grouse as of 2000 is shown in the inset. This distribution shows both the Greater or Northern Sage-Grouse (*C. urophaianus*) and the Gunnison Sage-Grouse (*C. minimus*), of southwestern Colorado and southeastern Utah (map provided by M. A. Schroeder, Washington Department of Fish and Wildlife).

Saskatchewan, but today occupy only about 6000 km^2 (Figure 1). The range contraction within Canada is primarily attributed to habitat loss.

Population Size and Trends

The most cost-effective and time-efficient method to estimate sage-grouse population size and trends is through lek counts. Lek counts involve counting the number of male sage-grouse displaying on a strutting ground during the spring mating season. The maximum number of males observed at each lek is then used as an index of population status (Beck and Braun 1980; Emmons and Braun 1984). Lek counts are used as indicators of population trends and to make population estimates for many lekking species, including all monitored sage-grouse populations.

Seasonal Lek Attendance

Adult males begin returning to leks once the latter are clear of snow. This typically occurs in mid-March in Alberta (Aldridge 2000). Breeding occurs over a one- to two-week period, as indicated by the peak in female attendance at leks: late March to early April in California (Bradbury et al. 1989), mid-April in Colorado (Petersen 1980), early April in Idaho (Autenrieth 1981), mid- to late April in Montana (Wallestad 1975; Jenni and Hartzler 1978), late April in Washington (Schroeder 1997), and in early April in Alberta (Aldridge 2000). The peak in male attendance typically occurs two to three weeks after peak female attendance/breeding at leks (Jenni and Hartzler 1978) (Figure 2). In general, about 50% of male sage-grouse attend leks prior to the peak in female attendance (breeding) (Figure 2). Radiotelemetry studies indicate a later peak in male attendance is due to yearling males first joining the lek two to three weeks after the peak of female attendance (Jenni and Hartzler 1978; Emmons and Braun 1984).

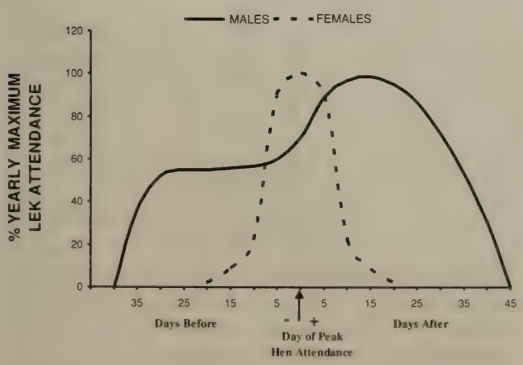


FIGURE 2. Predicted lek attendance by male and female sage-grouse (adapted from Jenni and Hartzler 1978). In Canada, peak female attendance usually occurs in the first week of April. If renesting efforts are high, female attendance is less Gausian in distribution, and female attendance is skewed to the right, overlapping more with peak male attendance.

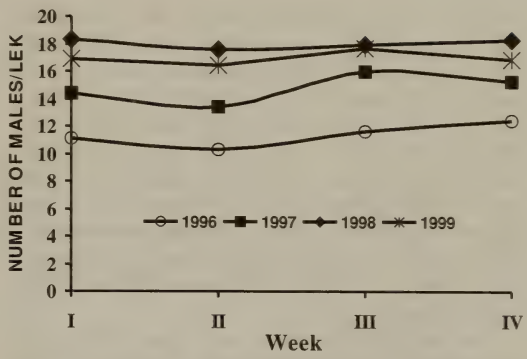


Figure 3. Weekly attendance by male Greater Sage-Grouse on leks in Alberta from 1996 to 1999. Week III represents the time when peak male attendance historically occurred in Alberta and Saskatchewan.

Detailed observations of male Greater Sage-Grouse lek attendance within each breeding season varied slightly from 1996 to 1999 in Alberta (Figure 3). Lek counts were divided into four seven-day periods, spanning the three 10-day periods recommended by Jenni and Hartzler (1978) and Beck and Braun (1980). The third week of counts occurred during the last week of April, when the peak in male attendance at leks should occur (Aldridge 1998) due to the arrival of yearling males (Dalke et al. 1963; Eng 1963; Jenni and Hartzler 1978). We obtained a maximum count for each lek during each of the four-week periods and used a two-way ANOVA to evaluate Week*Year interaction ($F_{9, 100} = 0.02$, $P > 0.10$), Week ($F_{3, 100} = 0.11$, $P > 0.10$) and Year effects ($F_{3, 100} = 1.24$, $P > 0.10$). The lack of significant differences in the attendance of males at leks over each year as a function of week suggests that yearling Greater Sage-Grouse are under-represented in the Canadian population. Capture data from Alberta also suggest that yearlings are under-represented in this population: only 25% (24/96) of captured birds were yearlings (Aldridge and Brigham 2001), compared to 44% of captures in Idaho (Dalke et al. 1963) and 46% of captures in Colorado (Braun and Beck 1985). Less than 18% of chicks in Canada survive to 50 days of age (Aldridge and Brigham 2001; C. L. Aldridge unpublished data), and the low recruitment for sage-grouse in Canada may be linked to poor chick survival.

Between-Year Trends

Greater Sage-Grouse lek counts within Alberta and Saskatchewan have been performed independently and, for this reason, we discuss population trends separately (Figure 4). In Alberta, surveys have been performed every two years on average since 1968, although gaps as long as five years have

occurred. During 1968/69, and in the early 1980s, numbers peaked and approached a total of 600 males counted on about 20 active leks (average > 25 males/lek) (Figure 4a, b). In Saskatchewan, the first surveys were performed in 1987 and 1988. They resulted in a total of nearly 600 males on about 30 active leks (average of about 20 males/lek) (Figure 4a, b). Since surveys in both provinces began, there has been a general decline in population numbers. In 1997, only 8 and 10 leks were active, supporting 122 and 61 males in Alberta and Saskatchewan, respectively (Figure 4a, b).

The most intensive lek counts were conducted in 1998 and 1999 in both provinces. Counts in Alberta resulted in a total of 147 males counted on eight active leks in 1998, and 140 males on eight leks in 1999 (Figure 4a, b). A similar trend occurred in Saskatchewan, where a total of 144 males were counted on 12 active leks in 1998 and a total of 131 males were counted on 10 leks in 1999 (W. C. Harris, personal communication; Figure 4a, b). We estimate the 1999 Canadian spring population was between 813 and 1204 individuals. Fall harvest (Braun 1998*) and winter population surveys (Beck 1977) in the United States suggest that the sex ratio for sage-grouse is female biased, ranging from 1.6 to 2.4 females per male. Thus, our estimates assume a spring sex ratio of two females for every male counted (C. E. Braun, personal communication). The low population estimate is simply the maximum number of males counted plus twice as many females. The high estimate assumes the same 2:1 sex ratio, but also takes into account the potential that only 90% of all leks are located and that only 75% of males attend leks at any given time (C. E. Braun, personal communication).

In 1987, counts were performed in both provinces, and a total of 915 males (400 in Alberta, 515 in Saskatchewan) were counted at 34 active leks (Figure 4a). This gives an estimated 1987 Canadian spring population of between 2745 and 4067 individuals. Based on 1999 estimates, the population has declined by as much as 80% since 1987. However, the 1987 total likely does not represent historic population levels, considering that counts in 1968 and 1981 in Alberta totaled 613 and 524 males respectively, and counts were also greater in Saskatchewan in 1988 (677 males) (Figure 4a). If these numbers are used to estimate a historic (≈ 1968) spring Greater Sage-Grouse population for the Canadian prairies (only within the current range), the population would have been between 3870 and 5733 individuals. This represents a potential decline of 86% within the currently occupied area over the last three decades. This is likely an underestimate, considering the historic range of Greater Sage-Grouse was potentially 90% greater than the currently occupied habitat (Figure 1). Increased search efforts over the last six years in both provinces likely resulted in higher count totals for the surveyed leks and may also mean that the population decline has been underestimated.

Using long-term lek count data for Alberta (Aldridge 1998, Alberta Sustainable Resource Development), we estimated the Greater Sage-Grouse population for each year from 1968 to 1999 using the previously discussed assumptions (Figure 4d). In the late 1960s, the Alberta population was between 1839 and 2724 birds. At its lowest levels in 1994, we estimate the population was between 210 and 311 individuals. In 1999, the population consisted of between 420 and 622 individuals. Thus, the Alberta population has declined from 1968 to 1999 by 66 to 92% (Aldridge 2000). This decline could be even greater, considering that in the early 1990s, Greater Sage-Grouse were known to exist outside of their current range, but these areas were not surveyed in past lek counts.

Active leks have also been decreasing in both Alberta and Saskatchewan. In the late 1960s, there were at least 21 active leks in Alberta and in 1988 there were 31 active leks in Saskatchewan (Figure 4b); 62 and 67% of leks have been abandoned in each province, respectively. The mean number of males per lek has also decreased in both provinces. Alberta averaged 29.2 males per lek in 1968, while Saskatchewan averaged 21.8 in 1988 (Figure 4c). By 1994, these numbers had decreased by 80% in Alberta and 64% in Saskatchewan to 5.8 and 7.8 males per lek, respectively.

Despite the overall decrease in population numbers, counts of males have remained somewhat stable over the last six years in both provinces (Figure 4). However, in both provinces, lek counts have been performed more rigorously over the last six years, and a concerted effort has been made to locate all leks (Aldridge 1998, 2000; W. C. Harris, personal communication). This increased effort may mask a continuing population decline.

Even though counts of males on leks over the last six years have remained relatively stable, the number of active leks in Canada decreased from 22 in 1994 to 18 in 1999 (Figure 4b). Over the same time period, the mean number of males counted per lek has more than doubled from 6.7 males/lek in 1994 to 15.1 in 1999 (Figure 4c). It is common for smaller subsidiary or satellite leks to be abandoned during population lows (Dalke et al. 1963), but the attendance at main lek complexes has increased over this time period. This suggests that changes have been occurring on the landscape, making smaller leks less desirable and causing birds to move to leks located in more suitable habitat.

Although it is evident the Canadian Greater Sage-Grouse population has declined, the exact rate of decline is difficult to ascertain, due to previously mentioned reasons and inconsistent sampling efforts (Aldridge 1998, 2000). It is also difficult to determine whether, in some years, leks that apparently

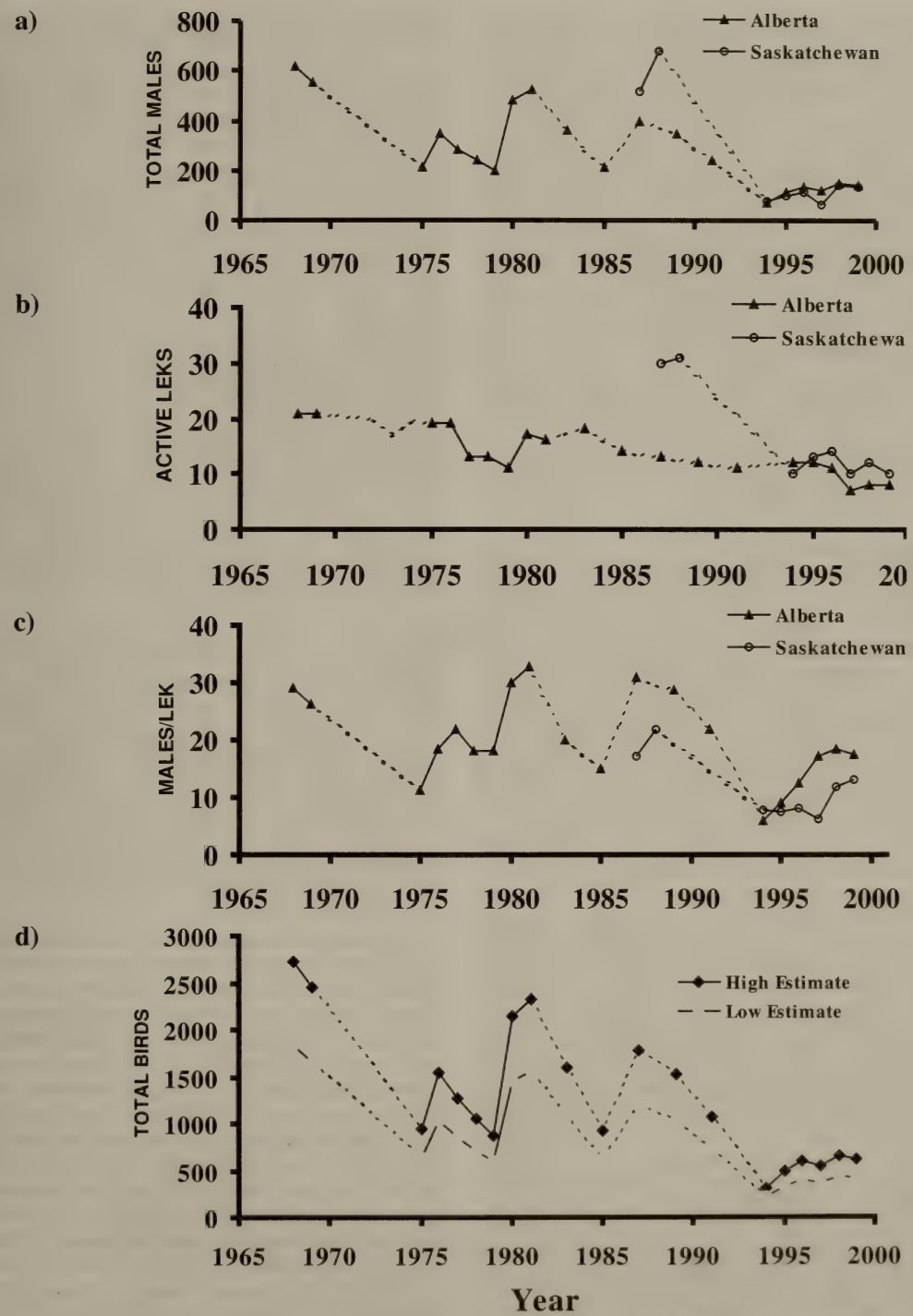


FIGURE 4. Population trends for Greater Sage-Grouse in Alberta and Saskatchewan from 1968 to 1999 shown as (a) total males, (b) active leks, and (c) males per lek. Long-term population estimates (d) are shown for the Alberta population only. Population estimates are based on maximum male lek counts. Low estimates assume a 2:1 female-biased sex ratio. High estimates assume that only 90% of all leks are located and that only 75% of males attend leks at any given time. For all graphs, years are not included when sampling efforts consisted of less than eight leks surveyed. Solid lines illustrate trends between years with consecutive data, and dashed lines estimate trends across years without data.

contained no birds were simply not checked, or could not be located and surveyed. Populations of sage-grouse also naturally fluctuate over periods of 7 to 10 years (Figure 4a), and these cycles (Patterson 1952; Rich 1985; Aldridge 1998) complicate population trends. Regardless of the rate of decline, it has been suggested that a minimum effective population size of 500 breeding individuals (Franklin 1980; Lande 1988) may be required to maintain sufficient genetic diversity to sustain a viable population. Given the lek mating system for Greater Sage-Grouse, the fact that only 10-15% of males actually breed in a given year (Anonymous 1997; C. E. Braun, personal communication), with each having different degrees of reproductive success, and the fact that many may die before successfully reproducing, a population size of 5000 Sage-Grouse may be required to maintain an effective population size of 500 breeding individuals (Braun 1995; Anonymous 1997; Aldridge 2000).

Limiting Factors

Although many different factors may have contributed to a reduction in sage-grouse numbers throughout the species' range, most deal with loss of suitable habitat and the degradation and fragmentation of remaining habitat (Schroeder 1997; Braun 1998; Schroeder et al. 1999). These alterations due to human encroachment and development as well as changes in climate and predator communities all may affect survival and productivity. A number of more localized disturbances, such as industrial development (Braun et al. 2002), have also contributed to the loss of suitable habitat. We address these potential limiting factors below.

Agricultural Practices

The demand for productive agricultural land in the 20th century resulted in massive sagebrush eradication programs. This decreased the range of sagebrush and, thus, potential sage-grouse habitat by an estimated 2.5 million ha from 1952 to 1977 (Braun et al. 1977). Since the late 1960s, when counts began in Alberta, cultivation of sagebrush-grasslands has likely resulted in the desertion of one lek (Braun et al. 2000) and possibly a second (C. L. Aldridge, personal observation). Ploughing in eastern Montana reduced Greater Sage-Grouse habitat by 16%, including 30% of the wintering range, and the population declined by 73% (Swenson et al. 1987). In addition, birds foraging in crop fields can be killed or injured by machines and other farm equipment (Patterson 1952; C. L. Aldridge, personal observation). Insecticides and herbicides are potentially lethal to sage-grouse (Blus et al. 1989), although their use on Canadian rangelands is limited.

Overgrazing has long been suggested as one of the main reasons for declining sage-grouse numbers (Dalke et al. 1963; Braun et al. 1977; Connelly and Braun 1997; Beck and Mitchell 2000). The removal of vegetation cover by cattle can have an impact on sage-grouse populations, either by reducing habitat suitability (Beck and Mitchell 2000) or by increasing the exposure of birds and nests to predators or extreme weather, all of which decrease survival and nest success (Watters et al. 2002). Important mesic sites in southern Alberta that provide lush forbs and insects as food resources for chicks are a limiting factor (Aldridge and Brigham 2002). Livestock grazing in these areas could therefore negatively impact chick survival and should be managed to optimize growth of forbs and grasses so as to increase chick survival (Beck and Mitchell 2000; Aldridge and Brigham 2002). Heavy grazing pressure during drought conditions could intensify these effects. Windberg (1975*) suggested that the declines indicated by lek counts in Alberta since 1968 correspond to an increase in intensity of livestock grazing in the southeastern part of the province. Grazing may simply decrease the carrying capacity of sage-grouse habitat (Windberg 1976*), especially in years with below average annual precipitation.

Human Disturbance

The unique spring mating rituals of sage-grouse attract naturalists, researchers, and interested members of the public each year. Nature photographers set up blinds at leks each spring in an attempt to photograph male sage-grouse in full breeding display. However, if birds are disturbed at leks, individuals will not return until the next day (C. L. Aldridge, personal observation). Continual disturbance at leks could result in abandonment of that site and may ultimately reduce breeding success and survival.

Predation

The predator community on the Canadian prairies has undergone drastic changes over the last 150 years. With the loss of the Plains Grizzly Bear (*Ursus horribilis*) and the Plains Wolf (*Canis lupus*), the Coyote *(Canis latrans)* is now the top predator. The Swift Fox (*Vulpes velox*) was once extirpated from Canada; however, a small population now exists after reintroduction. Raccoons (*Procyon lotor*), Striped Skunks (*Mephitis mephitis*), and Red Fox (*Vulpes vulpes*) have all increased on the prairies, especially in the last half century. Richardson's Ground Squirrels (*Spermophilus richardsonii*) are common nest predators of Greater Sage-Grouse in Alberta (Aldridge 2000; Watters et al. 2002). While Common Ravens (*Corvus corax*) do not coexist with Greater Sage-Grouse in Canada, American Crows (*Corvus brachyrhynchos*) and Black-billed Magpies (*Pica pica*) are common on the prairies and depredate both artificial (Watters et al. 2002) and natural Greater Sage-Grouse nests in Alberta (C. L. Aldridge, personal observation).

These changes in the predator community are tied to alterations in habitat structure and/or species composition. Predator control is not a viable option for managing prairie grouse populations, and enhancing or maintaining suitable habitat has been an effective management tool (see Schroeder and Baydack 2001).

Oil and Gas Exploration and Road Development

Oil and gas exploration and extraction within the Canadian range of Greater Sage-Grouse are key components of the economies of both Alberta and Saskatchewan. The removal of vegetation to construct well sites, access roads, pipelines, and associated facilities reduces and fragments suitable habitat. Human and mechanical activities at well sites may disrupt breeding and nesting activities. Even if sites are reclaimed, birds often fail to return to leks, as has been the case for at least one site in Alberta (C. L. Aldridge, personal observation). At least six of 32 traditional lek complexes in Alberta have been disturbed by oil and gas activities (Braun et al. 2002). Five of these leks are no longer active and the sixth lek complex, which originally had two large mating centers, has been reduced to one smaller site (Braun et al. 2002). Current records suggest that as many as 1500 wells have been drilled within the current range (4000 km^2) of the Greater Sage-Grouse in Alberta, and as many as one third of these are still producing (Braun et al. 2002).

A network of roads, trails, and power lines connects each well site with compressor stations and gas camps. Sage-grouse commonly fly into power lines and are often killed (Borell 1939; Patterson 1952; C. L. Aldridge, unpublished data). Poles associated with power lines provide perch sites for raptorial predators such as the Golden Eagle (*Aquila crysaetos*), which is an avid predator of sage-grouse (Schroeder et al. 1999). Each of these features not only reduces the suitability and availability of habitat for sage-grouse, but also fragments remaining habitat, providing corridors for predators such as Coyotes. Human activities are intense along these linear features which can disrupt breeding activities and negatively affect survival. Sage-grouse frequently travel on the ground, and when they cross roads and highways, many individuals are killed by vehicles (Patterson 1952). In the recent guidelines to manage sage-grouse populations and their habitat, Connelly et al. (2000) suggest that energy related facilities should be located >3.2 km from active leks (habitat protection is discussed below).

Climate

Although sage-grouse are large robust birds, harsh climatic conditions at the northern edge of the species' range likely affect populations. Short summers and particularly harsh winters likely reduce the ability of individuals to find enough food in winter months, especially given the low abundance of sagebrush in Canada (5-11%; Aldridge and Brigham 2002). This would result in decreased lipid reserves that are necessary for reproduction (Back et al. 1987; Hupp and Braun 1989) and possibly reduce overwinter survival (Back et al. 1987).

There is a positive relationship between spring precipitation and sage-grouse productivity (Gill 1966; Aldridge 2000). Years with below-average spring moisture result in less vegetation growth, apparently reducing sage-grouse nest success and reducing the availability of lush vegetation that is an important dietary component, especially for chicks (Aldridge and Brigham 2002). During the 1980s, spring precipitation was considerably below the long-term average (Aldridge 2000; Onefour Research Station, Environment Canada). This likely contributed to decreased productivity and resulted in reduced chick survival in Alberta (Aldridge and Brigham 2001). However, cold, wet spring precipitation events (rain or snow) can also result in increased nest failures (C. L. Aldridge, personal observation).

The effects of other limiting factors may be compounded during drought conditions. For example, consistent cattle-stocking rates in Canada during the droughts of the 1980s may have resulted in a substantial loss of vegetative cover, perhaps lowering nest success, increasing predation, and possibly lowering overwinter survival (Aldridge 1998, 2000). The impacts may have been particularly severe in more moist habitats, which supply important herbaceous growth during nesting and brood rearing. The probable increased attraction of cattle to these areas during drought conditions may decrease chick survival.

Protection

There is some indication that sage-grouse populations can be hunted with minimal effects on population size (Braun 1984; Braun and Beck 1985). However, given that most sage-grouse mortality occurs in the spring/summer (Schroeder et al. 1999) prior to fall hunting seasons, hunting is likely additive rather than compensatory. Thus, hunting small populations in fragmented areas may have significant implications. Greater Sage-Grouse were hunted in Saskatchewan only until 1938, but hunting continued in Alberta until the closure of the hunting season in 1996.

Federal

Due to declining numbers and limited distribution, Greater Sage-Grouse were listed as Threatened by COSEWIC in 1997. The status was upgraded to Endangered in 1998 (Hyslop 1998*) due to decreasing population numbers. However, until the federal Species At Risk Act (SARA) was passed in 2002 allowing habitat regulations to be put in place, the species was afforded little federal protection. Until then, protection of Greater Sage-Grouse was legislatively limited to that provided by provincial regulations.

British Columbia

Native Greater Sage-Grouse have not been observed in British Columbia since 1918 (Cannings et al. 1987). Attempts to reintroduce birds in the 1960s failed (Cannings et al. 1987), and the population was subsequently considered Extirpated (Hyslop 1998*).

Saskatchewan

Based on a declining population and a reduction in range, Greater Sage-Grouse were listed as a provincially Threatened species in Saskatchewan in 1987. In 1999, their status was changed to Endangered. Their habitat is now protected under the Wildlife Habitat Protection Act, which prevents lands containing Greater Sage-Grouse habitat from being sold or having their native vegetation cultivated.

In 1994, Saskatchewan implemented restrictions to limit development and disturbance at Greater Sage-Grouse lek sites. The Saskatchewan Wildlife Act was amended in 1997 to list and protect wild species at risk. With the 1999 Saskatchewan classification of Endangered, sage-grouse are now protected under the Saskatchewan Wildlife Act. These regulations provide protection for Greater Sage-Grouse, their nests, and leks sites. No developments within 500 m of leks are permitted and no construction activities within 1000 m of leks are allowed between 15 March and 15 May.

Alberta

Greater Sage-Grouse in Alberta were assigned a "Yellow" listing in 1991, meaning they were considered a species of concern due to naturally low populations, limited distribution, and limited available habitat (Anonymous 1991). In 1996 they were moved to the "Blue" list of species that may be at risk (Anonymous 1996). This designation was assigned due to the species' limited distribution, declining population numbers, and specific habitat requirements. In May 2000, the Alberta Endangered Species Conservation Committee listed Greater Sage-Grouse as Endangered under the Alberta Wildlife Regulations. Although Greater Sage-Grouse are still considered a game bird in Albert, they were afforded limited protection as a non-hunted species. As a provincially Endangered species, more rigid protection is available to protect against the capture, killing, or harming of individuals or their nests.

Greater Sage-Grouse habitat is not currently protected within the province of Alberta, although there is the potential for enforcement and protection of habitat to occur under other provincial legislation. Listing Greater Sage-Grouse as a provincially Endangered species places the Endangered Species Conservation Committee in charge of the species' recovery. It also affords significantly higher enforcement penalties and provides greater opportunity to protect Greater Sage-Grouse and their habitat.

Alberta Sustainable Resource Development has developed recommendations and land use guidelines which propose to limit activities surrounding sage-grouse leks throughout the year. From 16 June to 29 February, seismic activities, surveying, and monitoring would be prohibited within 100 m of leks, and from 1 March to 15 June, these activities would be prohibited within 500 m. Permanent developments would be prohibited within 1000 m of leks, regardless of time of year. However, these are recommendations only and cannot currently be legally enforced.

Evaluation

Connelly and Braun (1997) reported that range-wide decreases from prior to 1985 to after 1995 averaged 33% (range 17 to 47%). Braun (1998) suggested that overall breeding populations have declined by 45 to 80% since the early 1950s. The decline in Canada over the last 30 years may have been the most drastic: lek counts indicate a decline of between 66 and 92% since 1968 in Alberta, (Aldridge 2000). Greater Sage-Grouse now occur in less than 10% of their historic prairie range within Canada (Aldridge 2000), are listed as Endangered both federally and provincially (Alberta and Saskatchewan), and are considered extirpated from British Columbia.

Suitable Greater Sage-Grouse habitat in Canada is threatened with fragmentation and degradation from energy extraction activities, human developments and disturbances, and intensive livestock operations and agricultural operations. These threats may be magnified by climate change. The implications of each activity alone are poorly understood, yet the cumulative impact of these limitations may pose more serious threats to Greater Sage-Grouse. Changes in land management practices are probably necessary to save one of Canada's most endangered species. Further research into habitat requirements and the viability of sage-grouse is necessary to direct management practices within the conceptual framework of a collaborative adaptive management approach (Walters 1986). This will increase our understanding of Greater Sage-Grouse resource requirements and the viability of the species in Canada.

Acknowledgments

This research was supported financially and/or logistically by the Alberta Conservation Association, Alberta Sport Recreation Parks & Wildlife Foundation, Alberta Sustainable Resource Development, Cactus Communications (Medicine Hat, Alberta), Canada Trust Friends of the Environment Community Fund, Canadian Wildlife Foundation, Dennis Pattinson Memorial Scholarship, Ducks Unlimited Canada (North American Waterfowl Management Plan), Edgar A. Wahn Scholarship, Endangered Species Recovery Fund (World Wildlife Fund Canada, Canadian Wildlife

Service, and the Government of Canada's Millennium Partnership Program), Esso Imperial Oil (Manyberries, Alberta), Macnaughton Conservation Scholarship, Mountain Equipment Co-op, Murray Chevrolet Oldsmobile Cadillac (Medicine Hat, Alberta), Nature Saskatchewan, Saskatchewan Environment and Resource Management, Saskatchewan Stock Growers Association, Saskatchewan Wildlife Federation, Nova/Trans Canada Pipelines Ltd., and the University of Regina.

We thank T. L. Seida and M. E. Watters for their continued assistance and many other individuals who assisted with field activities. We thank the late Wayne Harris (Saskatchewan Environment and Resource Management) for assistance with the development of the Canadian range map and Saskatchewan lek count data. We thank the landowners who generously allowed us to conduct our research on their lands. C. E. Braun (Colorado Division of Wildlife), M. A. Schroeder (Washington Department of Fish and Wildlife), and A. J. Erskine provided useful comments on drafts of this manuscript.

Documents Cited (marked * in text)

Braun, C. E. 1998. North Park Sage Grouse harvest data, 1973-1998. Unpublished Report, Colorado Division of Wildlife, Fort Collins. 16 pages USA.

Hyslop, C. 1998. COSEWIC status report on Sage Grouse (*Centrocercus urophasianus*). Ottawa, Ontario. 38 pages.

Windberg, L. 1975. 1975 Breeding populations of Sage Grouse in Alberta. Unpublished Report, Alberta Department of Lands and Forests, Fish and Wildlife Division, Edmonton, Alberta. 7 pages.

Windberg, L. 1976. Alberta Sage Grouse populations (1975-76). Unpublished Report, Alberta Recreation, Parks and Wildlife, Fish and Wildlife Division, Edmonton, Alberta. 17 pages.

Literature Cited

Aldridge, C. L. 1998. Status of the Sage Grouse (*Centrocercus urophasianus urophasianus*) in Alberta. Alberta Environmental Protection, Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report Number 13, Edmonton, Alberta. 23 pages.

Aldridge, C. L. 2000. Reproduction and habitat use by Sage Grouse (*Centrocercus urophasianus*) in a northern fringe population. M.Sc. thesis. University of Regina, Regina, Saskatchewan. 109 pages.

Aldridge, C. L., and **R. M. Brigham.** 2001. Nesting and reproductive activities of Greater Sage-Grouse in a declining northern fringe population. Condor 103: 537–543.

Aldridge, C. L., and **R. M. Brigham.** 2002. Sage-Grouse nesting and brood habitat use in southern Canada. Journal of Wildlife Management 66: 433-444.

Anonymous. 1991. The status of Alberta wildlife. Publication Number I/413, Wildlife Management Branch Status Report, Alberta Forestry, Lands and Wildlife, Edmonton, Alberta. 49 pages.

Anonymous. 1996. The status of Alberta wildlife. Publication Number I/620, Alberta Environmental Protection, Natural Resources Service, Wildlife Management Division, Edmonton, Alberta. 44 pages.

Anonymous. 1997. Gunnison Sage Grouse conservation plan. Colorado Division of Wildlife. 108 pages.

Autenrieth, R. E. 1981. Sage Grouse management in Idaho. Idaho Department of Fish and Game, Boise. Wildlife Bulletin 9. 238 pages.

Back, G. N., M. R. Barrington , and **J. K. McAdoo.** 1987. Sage Grouse use of snow burrows in northeastern Nevada. Wilson Bulletin 99: 488-490.

Beck, T. D. I. 1977. Sage Grouse flock characteristics and habitat in winter. Journal of Wildlife Management 41: 18–26.

Beck, T. D. I., and **C. E. Braun.** 1980. The strutting ground count, variation, traditionalism, management needs. Proceedings of the Western Association of Fish and Wildlife Agencies 60: 558–566.

Beck, J. L., and **D. L. Mitchell.** 2000. Influences of livestock grazing on sage grouse habitat. Wildlife Society Bulletin 28: 986–992.

Blus, L. J., C. S. Staley, G. W. Pendleton, T. H. Craig, E. H. Craig, and **D. K. Halford.** 1989. Effects of organophosphorus insecticides on Sage Grouse in southeastern Idaho. Journal of Wildlife Management 53: 1139–1146.

Borell, A. E. 1939. Telephone wires fatal to Sage Grouse. Condor 41: 85–86.

Bradbury, J. W., R. M. Gibson, C. E. McCarthy, and **S. L. Vehrencamp.** 1989. Dispersion of displaying male Sage Grouse. II. The role of female dispersion. Behavioural Ecology and Sociobiology 24: 15–24.

Braun, C. E. 1984. Attributes of a hunted Sage Grouse population in Colorado, U.S.A. Pages 148–162 *in* 3rd International Grouse Symposium, World Pheasant Association. *Edited by* P. J. Hudson and T. W. I. Lovel. York University, United Kingdom.

Braun, C. E. 1995. Distribution and status of Sage Grouse in Colorado. Prairie Naturalist 27: 1–9.

Braun, C. E. 1998. Sage Grouse declines in western North America: what are the problems. Proceedings of the Western Association of State Fish and Wildlife Agencies 78: 139–156.

Braun, C. E., and **T. D. I. Beck.** 1985. Effects of changes in hunting regulations on Sage Grouse harvest and populations. Game Harvest Management Symposium 3: 335–343.

Braun, C. E., T. Britt, and **R. O. Wallestad.** 1977. Guidelines for maintenance of Sage Grouse habitats. Wildlife Society Bulletin 5: 99–106.

Braun, C. E., O. O. Oedekoven, and **C. L. Aldridge.** 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on Sage-Grouse. Transactions of the North American Wildlife and Natural Resources Conference 67: 337–349.

Cannings, R. A., R. J. Cannings, and **S. G. Cannings.** 1987. Birds of the Okanagan Valley, British Columbia. Royal British Columbia Museum. Morriss Printing Company Ltd., Victoria, British Columbia.

Connelly, J. W., and **C. E. Braun.** 1997. Long-term changes in Sage Grouse *Centrocercus urophasianus* populations in western North America. Wildlife Biology 3: 229–234.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and **C. E. Braun.** 2000. Guidelines to manage Sage Grouse populations and their habitats. Wildlife Society Bulletin 28: 967–985.

Crawford, J. A., and **R. S. Lutz.** 1985. Sage Grouse population trends in Oregon, 1941-1983. Murrelet 66: 69–74.

Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and **E. F. Schlatterer.** 1963. Ecology, productivity and management of Sage Grouse in Idaho. Journal of Wildlife Management 27: 810–841.

Emmons, S. R., and **C. E. Braun.** 1984. Lek attendance of male Sage Grouse. Journal of Wildlife Management 48: 1023–1028.

Eng, R. L. 1963. Observations on the breeding biology of male Sage Grouse. Journal of Wildlife Management 27: 841–846.

Eng, R. L., and **P. Schladweiler.** 1972. Sage Grouse winter movements and habitat use in central Montana. Journal of Wildlife Management 36: 141–146.

Franklin, I. R. 1980. Evolutionary change in small populations. Chapter 8, Pages 135–149 *in* Conservation biology: an evolutionary - ecological perspective. *Edited by* M. E. Soule and B. A. Wilcox. Sinauer Associates, Sunderland, Massachusetts.

Gill, R. B. 1966. Weather and Sage Grouse productivity. Colorado Department of Game, Fish and Parks, Denver, Colorado, Outdoor Information Leaflet. 37 pages.

Hupp, J. W., and **C. E. Braun.** 1989. Endogenous reserves of adult male Sage Grouse during courtship. Condor 91: 266–271.

Hupp, J. W., and **C. E. Braun.** 1991. Geographic variation among Sage Grouse in Colorado. Wilson Bulletin 103: 255–261.

Jenni, D. A., and **J. E. Hartzler.** 1978. Attendance at a Sage Grouse lek: implications for spring census. Journal of Wildlife Management 42: 46–52.

Kerwin, M. L. 1971. The status, behaviour, and ecology of the Sage Grouse in Saskatchewan. M.S. thesis, University of Regina, Regina, Saskatchewan. 104 pages.

Klebenow, D. A. 1969. Sage Grouse nesting and brood habitat in Idaho. Journal of Wildlife Management 33: 649–661.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241: 1455–1460.

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Sage Books, Denver, Colorado. 341 pages.

Peterson, B. E. 1980. Breeding and nesting ecology of female Sage Grouse in North Park, Colorado. M.S. thesis, Colorado State University, Fort Collins, Colorado. 86 pages.

Rich, T. 1985. Sage Grouse population fluctuations: evidence for a 10-year cycle. U. S. Department of the Interior, Bureau of Land Management, Boise, Idaho, Technical Bulletin 85-1. 20 pages.

Schroeder, M. A. 1997. Unusually high reproductive effort by Sage Grouse in a fragmented habitat in north-central Washington. Condor 99: 933–941.

Schroeder, M. A., J. R. Young, and **C. E. Braun.** 1999. Sage Grouse (*Centrocercus urophasianus*) *in* The Birds of North America, Number 425. *Edited by* A. Pool and F. Gill. The Birds of North America, Inc., Philadelphia, Pennsylvania. 28 pages.

Swenson, J. E., C. A. Simmons, and **C. D. Eustace.** 1987. Decrease of Sage Grouse after plowing of sagebrush steppe. Biological Conservation 41: 125–132.

Wallestad, R. O. 1975. Life history and habitat requirements of Sage Grouse in central Montana. Montana Department of Fish and Game, Helena, Montana. 65 pages.

Walters, C. J. 1986. Adaptive management of renewable resources. McGraw Hill, New York, New York, USA.

Watters, M. E., T. L. McLash, C. L. Aldridge, and **R. M. Brigham.** 2002. The effect of vegetation structure on the fate of artificial Greater Sage-Grouse nests. Ecoscience 9: 314–319.

Received 5 July 2000
Accepted 25 February 2003

Age Structure Differences in American Mink, *Mustela vison,* Populations under Varying Harvest Regimes

JACKSON S. WHITMAN

Alaska Department of Fish and Game, Wildlife Conservation Division, 1300 College Road, Fairbanks, Alaska 99835 USA

Whitman, Jackson S. 2003. Age structure differences in American Mink, *Mustela vison*, populations under varying harvest regimes. Canadian Field-Naturalist 117(1): 35–38.

Two American Mink populations were examined using canine tooth cementum annuli to assess age structure of harvested segments of the populations. Trapping mortality was different between these two populations. Comparisons are made with a Montana Mink population. I propose that furbearer managers can readily assess relative harvest pressures by analyzing the age structure of a Mink population, and offer management recommendations for populations displaying various age structures.

Key Words: American Mink, *Mustela vison*, age structure, cementum, harvest management, Alaska, Idaho, Montana.

Raw fur prices fluctuate dramatically due to unpredictable fashion trends. Thus, trapping intensity varies accordingly. American Mink (*Mustela vison*) are one of several species that are harvested throughout most of the United States and Canada (Eagle and Whitman 1987), and are considered a valuable fur resource (Deems and Pursley 1983). As early as 1938 it was recognized that intensive trapping can cause local declines in Mink populations (Errington 1938; McCabe 1949). However, furbearer managers are often at a disadvantage when assessing the status of various populations because of inadequate funding or staff.

In the absence of empirical population data, information presented here may provide managers with a reasonable, and relatively inexpensive, tool for assessing the status of wild Mink populations. Mink carcasses can easily be collected from trappers. In addition to assessing other parameters (diet, fat indices, sex ratios, reproductive status, etc.), canines or other teeth can be extracted, processed, and evaluated. A low incidence of juveniles in the harvested segment of the population may indicate low harvest pressure, poor recruitment, or may signal the presence of more severe environmental problems, such as the presence of toxic contaminants (Aulerich et al. 1974; O'Shea, et al. 1981), or food shortages.

Study Areas

Two American Mink populations were analyzed. A population in west-central Idaho (Upper Payette River drainage, Valley County) was studied between 1977 and 1980 (Whitman 1981). This population (Idaho) inhabited a high glacial valley, ranging from 1500-2000 m elevation in riverine habitat. Weather conditions were continental, typified by accumulations of snow in winter (mid-November through mid-April) and temperate, dry summers. Yearly precipitation averaged 64 cm. Temperature variations ranged from an average of –7.4°C in January to 17.1°C in July (Whitman 1981). This study area encompassed at least nine traplines that had been trapped annually for several decades at a moderate intensity.

A second Mink population in the Alexander Archipelago in southeast Alaska (Alaska), on Baranof and Chichagof Islands near Sitka, inhabited a marine coastal environment characterized by temperate, rainy conditions. Snow accumulations were highly variable, but rarely amount to more than 30 cm. Average annual precipitation was 219 cm, with temperature means of 3°C to 17°C in January and August, respectively. Carcass collections from this area were from the 1999/2000 trapping season, a year with no measurable snow accumulation. Area trappers only incidentally caught Mink while targeting American Marten (*Martes americana*) and River Otter (*Lontra canadensis*), so harvest pressures were extremely light.

Methods

Skinned Mink carcasses harvested during open seasons (November-January) were collected from trappers in both study areas. Lower canine teeth were extracted from animals suspected to be adults based on presence or absence of the suprasesamoid tubercle (Greer 1957), skull and bacular morphology, tooth wear, or skull suture characters. Juvenile animals (<8 months) were easily discernible from older age classes based on the above-mentioned osteological characters. Canines were sectioned, stained, and analyzed for number of cementum annuli (Matson's Laboratory, Milltown, Montana). Cementum annuli were assumed to represent the actual age of Mink in years (Eagle and Whitman 1987).

Logarithmic regression analysis was used to fit curves to age class data from harvested populations.

There were no significant differences between sexes in age class distribution, so sexes were pooled. Forty-two and 81 Mink were used for Idaho and Alaska samples, respectively.

Results and Discussion

Of 42 Mink from Idaho, 17 were adults (>1 year), for a juvenile:adult ratio of 1.47:1. In the Alaska sample, 45 of 81 animals were adults (0.8:1 ratio) (Table 1). The oldest animal in both populations was a single four-year-old, confirming reports of Mitchell (1961) in Montana, Gerell (1971) in Sweden, and Askins and Chapman (1984) in Maryland that population turnover largely occurred during a three-year period. Mitchell (1958) compared ages of Mink in intensively harvested areas versus unharvested areas, and reported dramatically different demographic parameters (juvenile:adult ratios of 4.5:1, and 0.3:1, respectively). In an attempt to clarify data reported by Mitchell (1958), and to compare those data with my own, I have assumed that his "adult" animals were all between the ages of 1 and 3 years.

In the Idaho study, I characterized Mink harvest as moderate; this harvest had been occurring for more than a decade prior to the investigation, and continued throughout the 1977-1980 study. Mink were common, but I assumed populations were below carrying capacity. In the Alaska investigation, trappers incidentally caught Mink in sets primarily designed for American Marten (*Martes americana*) and I judged their effects on Mink populations negligible. Because Marten did not exist on islands over most of the area, Mink harvests had been light prior to this investigation for at least five years. Thus, harvest pressures were assumed to be extremely light, and Mink existed at or near carrying capacity.

Comparison of age structure among populations (Figure 1) suggests that furbearer managers may be able to use age structure data as an indicator of the effects of harvest rate on Mink populations. If logarithmic curves can be fit to age structure data, steepness of the curves may be used to estimate harvest intensity. Obviously, Mink populations exist at widely differing densities throughout their range, largely dependent on carrying capacity of various habitats. High or low catches per unit area or per unit effort do not necessarily reflect high or low harvest pressure.

Using juvenile to adult ratios to assess harvest pressures can also be used without the time and expense of cementum analyses (Table 1) using my assessment of relative harvest pressure. In areas where the juvenile to adult ratio is greater than 2.0:1 and trapping is intense, managers should consider modifying regulations to reduce the harvest. However, where Mink trapping is incidental to other species, alignment of seasons is often an overriding

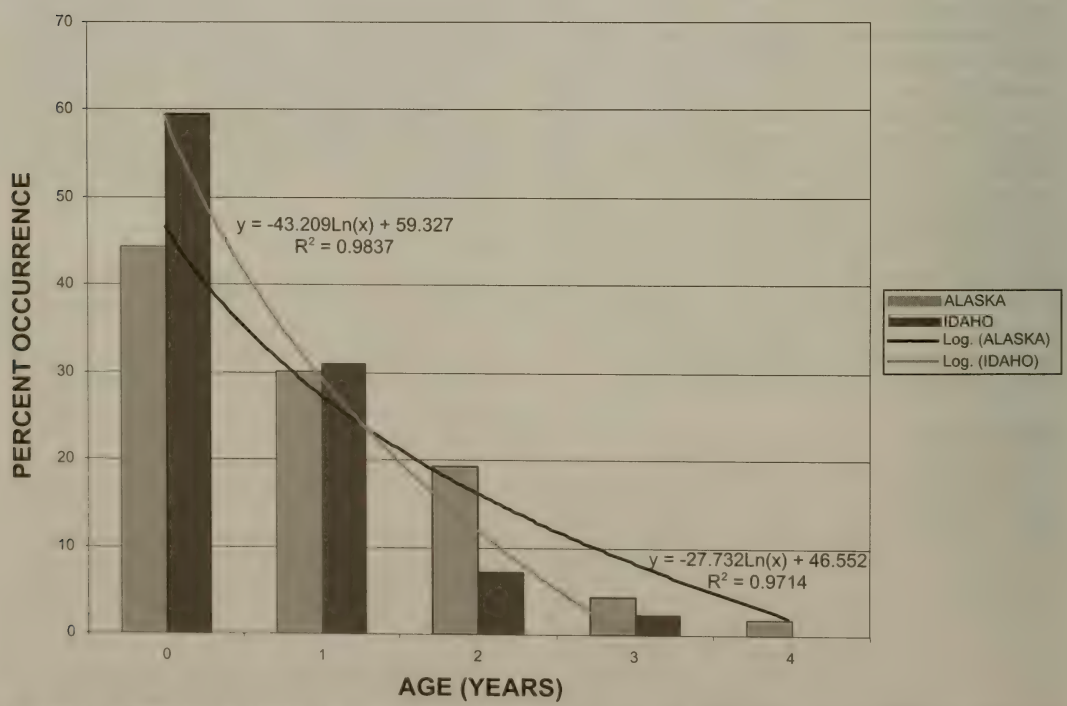


FIGURE 1. Comparison of harvest age classes for American Mink (*Mustela vison*) from Alaska, where no recent prior harvest had occurred, and from Idaho, where harvest was ongoing, but relatively moderate.

TABLE 1. American Mink juvenile:adult ratios in relation to harvest pressure from 4 study areas in North America, with management recommendations.

Relative Harvest	Author	Location	Juv:Ad Ratio	Possible Management Action
No Harvest	Mitchell, 1958	Montana	0.3:1	Nothing; Perhaps encourage harvest
Very Light Harvest	This Study, 2000	Alaska	0.8:1	Nothing
Moderate harvest	This Study, 1981	Idaho	1.5:1	Monitor future harvests closely
Heavy Harvest	Mitchell, 1958	Montana	4.5:1	Reduce or eliminate open seasons

management consideration. Additionally, where Mink harvest is incidental, adults may be more aggressive in patrolling their respective home ranges and thus more vulnerable to capture.

Interestingly, most authors agree that a high proportion of young in the harvest of American Marten is desirable (Strickland and Douglas 1987). Thus, from the data contained herein, there appears to be an incongruity in prescribed management of two closely related species. This can perhaps be explained by species differences in home range use and the relative numbers of dispersing and transient young-of-the-year animals in the populations. The greater vulnerability of young Marten is probably due to a number of factors, including lack of established home ranges and lack of experience. Young Mink, on the other hand, probably disperse from their natal ranges earlier than Marten, establishing home ranges before the trapping season commences (Gerell 1970), or may remain as residents in their natal home ranges (Harbo 1958).

Acknowledgments

I thank Linda Bergdoll-Schmidt for her assistance in numerous Mink carcass necropsies, often under malodorous conditions. The Idaho carcass collections were conducted through the University of Idaho Cooperative Wildlife Research Unit by the author with the supervision and encouragement of Maurice Hornocker. Wayne Melquist often provided field assistance and support. Alaska work was conducted as part of management operations by the author while working for the Alaska Department of Fish and Game. For their assistance in providing carcasses, I

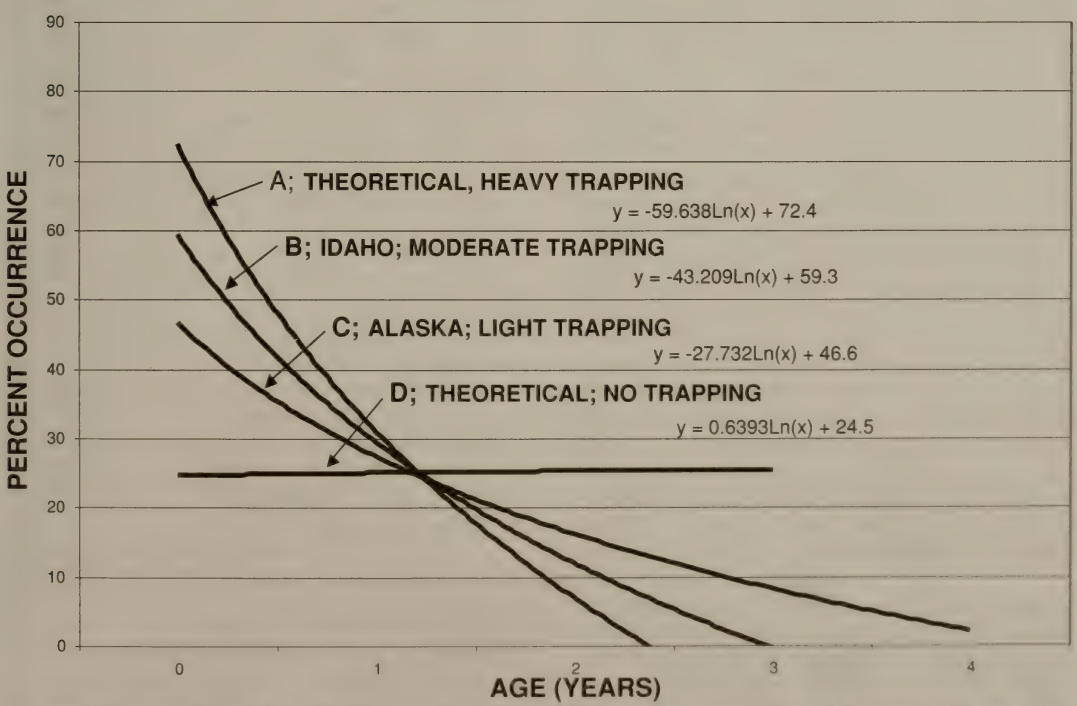


FIGURE 2. Theoretical (lines A and D) and actual (lines B and C) logarithmic regression lines of American Mink age distribution ranging from a population with very heavy trapping pressure (line A) through a population with no trapper exploitation (line D)

thank the many trappers who made the effort to contribute samples, especially Jim Bacon and Loyal, Mike, and Kevin Johnson. L. Johnson, W. B. Dinneford, J. Copeland and two anonymous reviewers provided valuable criticisms of this manuscript. Thanks are also extended to my supervisor, W. B. Dinneford, for allowing the latitude to explore furbearer population and management concerns.

Literature Cited

Askins, G. R., and **J. A. Chapman.** 1984. Age determination and morphological characteristics of wild mink from Maryland, USA. Zoologie Saugetierk 49: 182–189.

Aulerich, R. J., R. K. Ringer, and **S. Iwamoto.** 1974. Effects of dietary mercury on mink. Archive of Environmental Contamination and Toxicology 2: 43–51.

Deems, E. F., Jr., and **D. Pursley.** 1983. North American furbearers: a contemporary reference. International Association of Fish and Wildlife Agencies, Maryland Department of Natural Resources. 223 pages.

Eagle, T. E., and **J. S. Whitman.** 1987. Mink. Pages 614-624 *in* Wild Furbearer Management and Conservation in North America. *Edited by* M. Novak and J. Baker. Ontario Ministry of Natural Resources, Toronto.

Errington, P. L. 1938. The decline of a mink population. Journal of Mammalogy 19: 250–251.

Gerell, R. 1970. Home ranges and movements of the mink, *Mustela vison* Schreber in southern Sweden. Oikos 21: 160–173.

Gerell, R. 1971. Population studies on mink, *Mustela vison* Schreber, in southern Sweden. Viltrevy 8: 83–114.

Greer, K. R. 1957. Some osteological characters of known-age ranch minks. Journal of Mammalogy 38: 319–330.

Harbo, S. J., Jr. 1958. An investigation of mink in interior and southeastern Alaska. M.S. thesis, University of Alaska, Fairbanks. 108 pages.

McCabe, R. A. 1949. Notes on live-trapping mink. Journal of Mammalogy 30: 416–423.

Mitchell, J. L. 1958. Mink population study. Montana Fish and Game Department, Pittman-Robertson Project W-49-R-7, Project Report. 3 pages.

Mitchell, J. L. 1961. Mink movements and populations on a Montana river. Journal of Wildlife Management 25: 48–54.

O'Shea, T. J., T. E. Kaiser, G. R. Askins, and **J. A. Chapman.** 1981. Polychlorinated biphenyls in a wild mink population. Pages 1746–1751 *in* Proceedings of the Worldwide Furbearer Conference. *Edited by* J. A. Chapman and D. Pursley. Frostburg, Maryland.

Strickland, M. A., and **C. W. Douglas**. 1987. Marten. Pages 530-546 *in* Wild Furbearer Management and Conservation in North America. *Edited by* M. Novak and J. Baker. Ontario Ministry of Natural Resources, Toronto.

Whitman, J. S. 1981. Ecology of mink (*Mustela vison*) in west-central Idaho. M.S. thesis. Idaho Cooperative Wildlife Research Unit, University of Idaho, Moscow. 102 pages.

Received 30 October 2000
Accepted 30 June 2003

On the Vertical Zonation of Hair Lichens (*Bryoria*) in the Canopies of High-elevation Oldgrowth Conifer Forests

TREVOR GOWARD

Herbarium, Department of Botany, University of British Columbia, Vancouver, British Columbia V6G 2B1 Canada (Mailing address: Edgewood Blue, Box 131, Clearwater, British Columbia V0E 1N0 Canada)

Goward, Trevor. 2003. On the vertical zonation of hair lichens (*Bryoria*) in the canopies of high-elevation oldgrowth conifer forests. Canadian Field-Naturalist 117(1): 39–43.

Three vertical zones of *Bryoria* abundance are recognized in the canopies of mid- and upper-elevation oldgrowth conifer forests in southern inland British Columbia. Zone A, with virtually no *Bryoria*, is restricted to the lower trunk and lowermost branches, where its upper boundary (the "A/B threshold") corresponds roughly to the maximum settled depth of the winter snowpack. Zone B is located directly above Zone A, and supports *Bryoria* in variable amounts ranging from negligible to heavy; its upper boundary is defined by an abrupt increase in *Bryoria* at the "B/C threshold". Above this is Zone C: a well-ventilated region supporting maximum *Bryoria* loadings consisting predominantly of the nonsorediate species *B. fremonti*, *B. pseudofuscescens*, and *Nodobryoria oregana*. *Bryoria* loadings in Zone B benefit from litterfall from Zone C, in the absence of which, Zone B would predominantly support only the sorediate species *B. fuscescens* and *B. glabra*. Winters of exceptionally deep snow cause marked upward shifts in the A/B threshold, presumably resulting in reductions in the early-winter availability of *Bryoria* to Mountain Caribou. This reduced forage is expected to prolong early-winter migrations to lower elevations, where Caribou depend on lichen-rich oldgrowth forests. The existence of such forests is hypothesized to be integral to the long-term maintenance of healthy caribou populations.

Key Words: *Bryoria fremontii, Bryoria pseudofuscescens, Nodobryoria oregana,* arboreal lichens, conifer forests, Woodland Caribou, *Rangifer tarandus,* mountain ecotype, Wells Gray Provincial Park, British Columbia.

The mid- and upper-elevation oldgrowth conifer forests of southern inland British Columbia provide winter habitat for the mountain ecotype of the Woodland Caribou (*Rangifer tarandus caribou*). Unlike the more northerly Barrenground Caribou, Mountain Caribou are behaviourally adapted to survival in regions of deep snow (Paquet 1997). In winter, when deepening snows render terrestrial forage unavailable, these animals subsist predominantly on a diet of arboreal hair lichens (Edwards and Ritcey 1960; Rominger and Oldemeyer 1990).

At least 13 species of arboreal hair lichens occur within the winter range of Mountain Caribou, i.e., ten species of *Bryoria*, two of *Nodobryoria*, and one of *Alectoria* (Goward, in preparation). The extent to which a given species is utilized depends not only on its overall availability at foraging heights, but also on the foraging behaviour of Caribou. For example, the green hair lichen *Alectoria sarmentosa*, though most abundant in the lower canopy (Campbell and Coxson 2001), tends to be avoided by Caribou (Rominger et al. 2000). Rominger et al. (1996) emphasize that wintering Caribou forage preferentially on *Bryoria*, which they seek out especially in sites supporting heavy loadings.

Little is known about the relative contributions of individual species of lichen to the winter diets of Mountain Caribou, most previous studies having focussed at the genus level. However, recent work by Goward and Campbell (in preparation) suggests that *B. fuscescens* and, to a lesser extent, *B. glabra* are the most common *Bryoria* species at foraging heights, at least in mid-successional stands. Still, because neither of these species dominates in the high-biomass sites most attractive to Caribou (Goward and Wright, in preparation), their contribution to caribou winter forage is therefore probably less than would be predicted based on frequency alone.

Much more abundant in preferred Caribou foraging sites are *B. fremontii*, *B. pseudofuscescens*, and *Nodobryoria oregana* (Goward, in preparation). These are long, pendulous lichens that characteristically lack soredia and apothecia, and hence rely on thallus fragmentation as the primary mode of reproduction. Related to this, all of these species exhibit indeterminate growth, their thalli being capable of elongating indefinitely. In practice, however, these species seldom measure more than about 10 to 30 cm long (except to 90 cm long in *B. fremontii*: Brodo and Hawksworth 1977). Maximum thallus size is reached once branch growth rates come into equilibrium with branch loss through fragmentation. The best available information suggests that, depending on initial fragment size, this state of equilibrium can be attained in under 20 years (Esseen and Renhorn 1996; Goward, unpublished data).

Much remains to be learned about the distribution of hair lichens in oldgrowth forests. Given the reported preference of wintering Caribou for heavy *Bryoria* loadings, it would be useful to determine under what conditions such loadings develop in por-

tions of the canopy accessible to these animals. The main objective of this paper is to address this question with respect to mid- and upper-elevation oldgrowth Engelmann Spruce (*Picea engelmannii*) - Subalpine Fir (*Abies lasiocarpa*) (ESSF) forests in southern inland British Columbia. More specifically, it attempts to summarize the vertical apportioning of *Bryoria* in these forests. The observations reported here build on the earlier findings of Goward (1998), and are based on incidental field studies carried out over a period of ten years in southern inland British Columbia, especially in the Sicamous Creek Research Forest (50°49′N, 118°50′W) (Hollstedt and Vyse 1997), and in Wells Gray Provincial Park (51°51′N, 119°52′W) (Goward and Ahti 1992).

"Mid-elevation" refers to those portions of the ESSF between about 1400 and 1900 m, with a more or less continuous forest cover. "Upper-elevation" forests occur between about 1900 and 2100 m, and are transitional to the alpine tundra; they are much more open and, as a consequence, better ventilated. These elevational boundaries are representative of conditions at about 52°N; north of this, they gradually descend, whereas to the south they climb.

Vertical Patterns of *Bryoria* in the Forest Canopy

The vertical apportioning of *Bryoria* in the canopies of mid- and upper-elevation oldgrowth forests can be divided into three zones. For convenience, these zones will be referred to here as Zone A, Zone B, and Zone C (Figure 1). The boundaries separating these zones are termed "thresholds".

Zone A

Zone A is restricted to the lowermost trunk and branches, often extending upwards to 2-4 m above the ground. Here hair lichens are essentially absent. Goward (1998) has suggested that the inability of hair lichens to establish in this portion of the canopy reflects a pronounced physiological sensitivity to prolonged wetting as a consequence of burial under the winter snowpack (see also Coxson and Curteanu 2002). The upper limits of Zone A (henceforth the "A/B threshold") correspond roughly to the upper surface of the late winter snowpack (Taylor 1922).

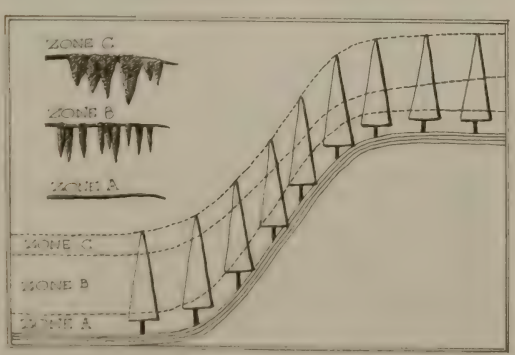


FIGURE 1. Vertical zonation of *Bryoria* in the canopies of high-elevation oldgrowth forests in southern British Columbia (see text).

Winter snowpacks can vary markedly from year to year. Reflecting this, the A/B threshold is subject to periodic shifts in vertical position. The most dramatic upward shifts are initiated during winters of exceptionally deep snow, when the A/B threshold can be elevated by a metre or more (Goward, in preparation). Once established, an elevated A/B threshold might require several years to recolonize downward to its original "average" position (Goward, in preparation). The rate of recovery is presumably linked to the rate of thallus recruitment from higher in the canopy.

Determining the "average" vertical position of the A/B threshold can be difficult, owing to the uneven snow surface beneath the canopies of trees. For general purposes, the trunks of large leaning trees provide a convenient point of reference. Here the upper limits of Zone A are denoted by the lower trimline of *Alectoria* and *Bryoria*.

Zone B

Situated immediately above Zone A is Zone B. In general, the "A/B threshold" is defined by a sudden upward increase in hair lichen biomass. Notwithstanding this, *Bryoria* biomass in Zone B is also highly variable. Within a given site, thallus loadings appear to be controlled by two opposing factors, both pertaining primarily to the nonsorediate species. These are ongoing inoculation from Zone C (see below), and periodic die-backs. Die-backs occur as a result of prolonged wetting, and result in the presence of necrotic thalli: a characteristic feature of Zone B (Goward 1998; Campbell and Coxson 2001). Prolonged thallus wetting is most frequent toward the branch tips (Goward 1998), where it is mediated by several small-scale phenomena, including needle cast, increasing branch length higher in the canopy, the seasonal development of snow clumps ("qali"), crown breakage, and, at the stand level, the stochastic formation of canopy gaps. These and other factors — especially prolonged wet, cool weather — ensure that *Bryoria* biomass in Zone B is unstable, fluctuating both spatially and temporally.

Depending on ventilaton, Zone B can vary considerably in vertical amplitude: in closed stands it occupies virtually the entire crown, while in open stands it can be limited to the lowermost branches. In highly exposed situations, this zone can be lacking altogether (see Zone C).

Zone C

The upper limit of Zone B is marked by a dramatic increase in *Bryoria* biomass, a trend most readily observed in the canopies of old trees. Above this is Zone C: the zone of optimum *Bryoria* development.

The upward increase in *Bryoria* biomass is accompanied by subtle change in thallus morphology, at least among the nonsorediate species. In Zone B these species have long, narrow thalli that somewhat resemble the teeth of a comb. In Zone C, by contrast, they attach more broadly to the supporting branch, hence calling to mind triangular pennants or tattered curtains (Figure 1). This shift in thallus form presumably reflects a transition from suboptimal growing conditions in Zone B (where thalli are unable to develop laterally along the supporting branch) to optimal conditions in Zone C (where lateral growth is more pronounced).

Three additional B/C markers can be observed. The first of these involves the ability of healthy thalli to grow out towards the foliated branch tips in Zone C — a phenomenon not seen in Zone B, where healthy thalli are essentially restricted to the defoliated branch portions. The second marker is the general absence, in Zone C, of the necrotic thalli often so common in Zone B, especially toward the branch tips. And finally, the B/C threshold roughly corresponds to the upper limits of well-developed thalli of *Alectoria sarmentosa*. It should be noted, however, that this species is strongly dispersal-limited in the ESSF, and hence does not always occupy its full potential vertical range, even in oldgrowth stands; its upper trimline must therefore be interpreted with caution (Goward, in preparation).

The B/C threshold can be rather diffuse, sometimes spanning two metres or more. It also varies markedly in vertical position across short horizontal distances, often even within the canopy of a single tree. Such variations are correlated with ventilation. In forested sites, the B/C threshold occurs mostly in the middle or upper canopy, though in more exposed sites, it can descend virtually to the upper limits of Zone A. In the absence of a well-developed Zone B, the boundary between zones A and C can be referred to as the A/C threshold. A parallel trend is discernible also at the landscape level, with an elevated B/C threshold at the foot of hillslopes, and a much lower threshold on upper slopes and hillcrests (Figure 1).

Unlike Zone B, which in the ESSF is present in forests of all ages, a well-developed Zone C is usually restricted to oldgrowth forests; young stands support only meagre *Bryoria* loadings in Zone C (Goward and Campbell, in preparation). Zone C also differs from Zone B in supporting more consistently heavy *Bryoria* loadings. Presumably this reflects the uninterrupted accumulation of *Bryoria* biomass over extended periods; i.e., without the depleting influence of periodic die-backs, as in Zone B.

Zone C is invariably associated with exposure to high levels of ventilation, leading to significant loss of hair lichen biomass as a result of thallus fragmentation (Goward 2003). Presumably most thallus fragments fall to the ground and are lost to decay (Coxson and Curteanu 2002). Some, however, are intercepted by branches lower in the canopy, over time accumulating to moderate or even heavy loadings. Litterfall from Zone C can thus provide a primary source of *Bryoria* biomass in Zone B — an observation consistent with the much greater incidence of nonsorediate *Bryoria* thalli in the lower canopies of forests with a well-developed Zone C (Goward, in preparation). In the absence of litterfall from Zone C, heavy *Bryoria* loadings are unlikely to develop in Zone B. The relationship between Zones C and B thus recalls the source-sink population model of Pulliam (1998), in which high quality source populations (as in Zone C) export propagules to low quality sink populations (as in Zone B). The latter populations are thus dependent for their long-term persistence upon the former.

Implications for Caribou Winter Ecology

This paper has presented four observations pertinent to the vertical zonation of *Bryoria* biomass in mid- and upper-elevation oldgrowth forests in British Columbia: (1) *Bryoria* loadings are consistently heavy in well-ventilated portions of the canopy (Zone C); (2) *Bryoria* loadings are more variable in poorly ventilated portions of the canopy (Zone B); (3) hair lichens (including *Bryoria*) are virtually absent from portions of the canopy buried by the winter snowpack (Zone A); and (4) winters of exceptionally deep snow induce marked upward shifts in the vertical extent of Zone A. It is emphasized that these findings are based on field observations, and must hence be considered preliminary until confirmed by careful quantitative studies. From a management perspective, however, it might be useful to draw attention to two potential implications arising from them, and pertaining to Mountain Caribou.

Bryoria availability

The widespread occurrence of a well-developed Zone C is pivotal to the winter ecology of Mountain Caribou. These animals benefit from Zone C both directly and indirectly. Direct benefits include access to heavy *Bryoria* loadings in a range of settings, including the upper canopies of downed trees, the lower canopies of standing trees, and, in the case of litterfall, the snow surface. A potentially important indirect benefit of Zone C is the continuous release of *Bryoria* fragments into Zone B. Here it can be noted that heavy *Bryoria* loadings are likely to occur in Zone B only in proximity to trees supporting a well-developed Zone C (Goward and Wright, in preparation).

The relative availability of Zone C to caribou varies markedly with elevation. Upper ESSF forests, for example, have an open, clumpy stand structure permitting the B/C threshold to descend, on average,

to the lower portions of the middle canopy. This results in a vertically broad Zone C that in turn contributes copious litterfall to Zone B. At lower ESSF elevations, stand structure is more closed. Here the B/C threshold occurs proportionately higher in the canopy, with the result that Zone C, being vertically reduced, contributes strikingly less *Bryoria* biomass to Zone B. Not surprisingly, heavy *Bryoria* loadings at foraging heights are much more localized in these lower ESSF forests. It must be stressed that the above comments pertain to oldgrowth stands; younger ESSF stands generally suuport only an incipient Zone C, with very low biomass (Goward and Campbell, in preparation).

Seasonal migrations

Beginning in late October or early November, many caribou herds move downwards into the valleys from their high-elevation summer ranges. Such early-winter migrations are well documented (Edwards 1954; Seip 1992), and have in the past usually been interpreted exclusively as a response to deep, unsettled snow (Edwards and Ritcey 1959; Antifeau 1987). However, another, probably complementary explanation is also possible: the migrations could be triggered by the temporary unavailability of *Bryoria* at upper elevations.

Caribou are capable of foraging to heights of only about 1.7 - 2 m (B. McLellan, personal communication). In forests with A/B (and A/C) thresholds higher than this, early winter is doubtless a difficult period for these animals. With terrestrial food sources rendered inaccessible by deepening snows, caribou must either subsist on lichen litter (mostly on downed trees), or else migrate to lower elevations where lesser snow packs permit access to arboreal lichens and terrestrial food sources (Rominger et al. 2000).

How long caribou remain at lower elevations during a given winter is probably a function of two variables pertaining to their upper ESSF habitats: (1) the vertical position of the A/B threshold; and (2) the rate of snow accumulation during a given winter. In principle, Caribou should return to their upper ESSF winter ranges only upon the development of a snow platform sufficiently elevated to support them at foraging heights. Winters of rapid snow accumulation would thus permit them to return earlier, while late winters could delay their return for weeks or possibly months.

It has already been observed that years of exceptionally heavy snows prompt upward shifts in the A/B threshold. In subsequent winters, especially if the snowpack is late in accumulating, caribou are probably obliged to remain at valley elevations much longer than normal. Such winters can be predicted to be highly stressful for these animals, first because they are at higher-than-average risk of encountering predators, and second, because as oldgrowth forests continue to be replaced by young plantation stands, the likelihood of locating *Bryoria*-rich windthrown trees must also decline (Goward 2002). A similar situation might arise even in regions of lighter snowpacks, where typically non-migratory herds are from time to time forced to lower elevations. Such reflections, though admittedly speculative, emphasize the potentially crucial role played in Mountain Caribou winter ecology by lowland oldgrowth forests.

Acknowledgments

This study forms part of the Sicamous Creek Silvicultural Systems Project. Field studies were funded in part by the British Columbia Ministry of Forests. Additional funding was received through Susan Hall, of Parks Canada, as well as through Michael Burwash, of the British Columbia Ministry of Environment, Lands, and Parks. I thank Ian Eakins and Wes Bieber for transportation in the field, and André Arsenault, Wes Bieber, Jim Blueschke, Kristi Iverson, Ken MacKenzie, Bruce McLellan, John Surgenor, and especially Ken Wright for valuable assistance, as well as for stimulating discussion. Participants in the Second Annual *Bryoria* Workshop (Wells Gray Provincial Park, March 2000) also tested many of the ideas presented here. Susan Stevenson, Matthew Stewart, and Ken Wright kindly reviewed an earlier version of the manuscript.

Literature Cited

Antifeau, T. D. 1987. The significance of snow and arboreal lichens in Wells Gray Provincial Park with special reference to their importance to mountain caribou (*Rangifer tarandus caribou*) in the North Thompson watershed of British Columbia. M.Sc. thesis, University of British Columbia. 142 pages.

Brodo, I. M., and **D. L. Hawksworth.** 1977. *Alectoria* and allied genera in North America. Opera Botanica 42: 1–164.

Campbell, J., and **D. S. Coxson.** 2001. Canopy microclimate and arboreal lichen loading in subalpine spruce-fir forest. Canadian Journal of Botany 79: 537–555.

Coxson, D. S., and **M. Curteanu.** 2002. Decomposition of hair lichens (*Alectoria sarmentosa* and *Bryoria* spp.) under snowpack in montane forest, Cariboo Mountains, British Columbia. Lichenologist 34: 395–402.

Edwards, R. Y. 1954. Fire and the decline of a mountain caribou herd. Journal of Wildlife Management 18: 521–526.

Edwards, R. Y., and **R. W. Ritcey.** 1959. Migrations of caribou in a mountainous area in Wells Gray Park, British Columbia. Canadian Field-Naturalist 73: 21–25.

Edwards, R. Y., and **R. W. Ritcey.** 1960. Foods of caribou in Wells Gray Park, British Columbia. Canadian Field-Naturalist 74: 3–7.

Esseen, P.-A., and **K.-E. Renhorn.** 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. Ecological Applications 6: 228–238.

Goward, T. 1998. Observations on the ecology of the lichen genus *Bryoria* in high elevation conifer forests. Canadian Field-Naturalist 112: 496–501.

Goward, T. 2002. Hair lichens, snowpack variation and the fate of the Mountain Caribou: the LSC hypothesis. Pages 41-42 *in* Mountain Caribou in 21st Century Ecosystems. *Edited by* Anonymous. Columbia Mountains Institute of Applied Ecology, Revelstoke, British Columbia.

Goward, T. 2003. On the dispersal of hair lichens (*Bryoria*) in high-elevation oldgrowth conifer forests. Canadian Field-Naturalist 117(1): 44–48.

Goward, T., and **T. Ahti.** 1992. Macrolichens and their zonal distribution in Wells Gray Provincial Park and its vicinity, British Columbia, Canada. Acta Botanica Fennica 147: 1–60.

Hollstedt, C., and **A. Vyse.** *Editors.* 1997. Sicamous Creek Silvicultural Systems Project: Workshop Proceedings. April 24-25, 1996. Kamloops, British Columbia, Canada. Research Branch, British Columbia Ministry of Forests Working Paper 24/1997. Victoria, British Columbia.

Paquet, M. 1997. Toward a mountain caribou management strategy for British Columbia. Background report. Wildlife Branch, British Columbia Ministry of Environment, Lands and Parks. Victoria. 72 pages.

Pulliam, H. R. 1998. Sources, sinks, and population regulation. American Naturalist 132: 652–661.

Rominger, E. M., and **J. L. Oldemeyer.** 1990. Early-winter diet of woodland caribou in relation to snow accumulation. Canadian Journal of Zoology 68: 2691–2694.

Rominger, E. M., C. T. Robbins, and **M. A. Evans.** 1996. Late-winter foraging dynamics of woodland caribou. Journal of Wildlife Management 60: 719–728.

Rominger, E. M., C. T. Robbins, M. A. Evans, and **D. J. Pierce.** 2000. Autumn foraging dynamics of woodland caribou in experimentally manipulated habitats, northeastern Washington, USA. Journal of Wildlife Management 64: 160–167.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology 70: 1494–1503.

Taylor, W. 1922. Lichen growth and snow depth. Canadian Field-Naturalist 36: 113–114.

Received 1 November 2000
Accepted 5 May 2003

On the Dispersal of Hair Lichens (*Bryoria*) in High-Elevation Oldgrowth Conifer Forests

TREVOR GOWARD

Herbarium, Department of Botany, University of British Columbia, Vancouver, British Columbia V6G 2B1 Canada (Mailing address: Edgewood Blue, Box 131, Clearwater, British Columbia V0E 1N0 Canada)

Goward, Trevor. 2003. On the dispersal of hair lichens *(Bryoria)* in high-elevation oldgrowth conifer forests. Canadian Field-Naturalist 117(1): 44–48.

Arboreal hair lichens belonging to the genus *Bryoria* provide crucial winter food for the threatened Mountain ecotype of the Woodland Caribou. Earlier studies suggest that the reliance of many *Bryoria* species on thallus fragmentation as a primary mode of reproduction can lead to low dispersal rates. This paper examines the occurrence of thallus fragments over a snow-covered subalpine meadow following a late winter windstorm of moderate force. Fragment densities were greatest immediately downwind of the forest edge, but remained substantial even at a distance of 2 km. This suggests that dispersal is not limiting for at least some *Bryoria* species at subalpine elevations. It is proposed that the ecological requirement of *Bryoria fremontii* and *B. pseudofuscescens* for well-ventilated habitats considerably enhances their ability to inoculate young, regenerating stands over considerable distances. Their observed general absence in young trees is probably a function of substrate limitations rather than of limitations of dispersal.

Key Words: *Bryoria fremontii, Bryoria pseudofuscescens, Nodobryoria oregana*, arboreal lichens, conifer forests, wind dispersal, Wells Gray Provincial Park, British Columbia.

Mountain Caribou are a globally threatened ecotype of the Woodland Caribou *(Rangifer tarandus caribou)* (see Thomas and Gray 2001*). Restricted to southern inland British Columbia and adjacent Washington and Idaho (Paquet 1997), these animals spend much of each winter at upper forested elevations. Here snowpacks two to four metres deep make cratering for terrestrial forage impractical; to survive, wintering Caribou must depend on a nearly exclusive diet of arboreal hair lichens (Edwards and Ritcey 1960; Rominger et al. 1996).

Thirteen species of hair lichens are known from the upper-elevation Engelmann Spruce *(Picea engelmannii)* — Subalpine Fir *(Abies lasiocarpa)* forests (henceforth ESSF) of inland British Columbia (Goward and Ahti 1992; and later observations). Ten of these are members of the genus *Bryoria,* while two belong in *Nodobryoria,* and one in *Alectoria.* All are pendulous species with a hair-like morphology, and all colonize the branches of conifers.

In boreal and montane ecosystems, hair lichens are typically more abundant in oldgrowth forests than in younger forest types (Esseen et al. 1996; McCune 1993; Peterson and McCune 2001). The inability of hair lichens to accumulate to heavy loadings in young forests can potentially be attributed to one or more of four causes: (1) unsuitable bark chemistry associated with young branches; (2) slow growth rates; (3) unsuitable microclimatic conditions; and (4) inefficient mechanisms of dispersal. The respective roles of these mechanisms in the distributional ecology of hair lichens in high-elevation oldgrowth forests are briefly discussed below.

Branch Chemistry

Young tree branches occur in young and old stands alike. If the chemistry of young branches were truly limiting to hair lichen establishment, then hair lichens should invariably be lacking from this substrate. Yet young branches in old stands can actually support rather high loadings of hair lichen, at least under well-ventilated conditions (Goward 1998). On this evidence, bark chemistry seems unlikely to be prohibitive to hair lichen development in the ESSF. Recent research, however, suggests that an elevated bark pH may adversely affect hair lichen establishment in some lower elevation forests (Goward and Arsenault 2003).

Growth Rates

Lichens are often assumed to be slow-growing organisms. Recent studies by Stevenson (1979), Esseen et al. (1996), and McCune et al. (1996), however, indicate that hair lichens grow more rapidly than previously thought, with annual increments in the order of 5% to 30%. This is consistent with the observation that at least some *Bryoria* species attain mature proportions in under 20 years (Goward, unpublished). Slow growth rates per se are thus unlikely to be responsible for the low hair lichen loadings characteristic of young forests.

Microclimate

Goward (1998) has suggested that hair lichen biomass is controlled primarily by a pronounced sensitivity to prolonged wetting. Viewed from this perspective, within-canopy shifts in hair lichen loadings can be expected to correspond to age-related changes

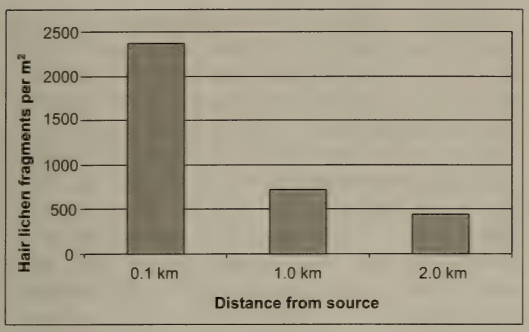


FIGURE 1. Wind-scattered hair lichen fragments in relation to distance from source, 7 April 1996, Fight Lake Meadow, Wells Gray Provincial Park, British Columbia.

in forest structure. As a forest ages, the creation of canopy gaps exposes hair lichens to gradually increasing levels of ventilation. At the same time, the centrifugal architecture of conifers ensures an increasing incidence of microniches sheltered from frequent wetting. Many hair lichens, especially in the genus *Bryoria,* appear to be specially adapted to these conditions (Campbell and Coxson 2001), suggesting that microclimate can play a significant role in the stand-level distribution of these species.

Dispersal

Few quantitative studies involving hair lichen dispersal have been undertaken to date. In a field trial in 10-15-year-old Douglas-fir *(Pseudotsuga menziesii)* plantations on Vancouver Island, Stevenson (1988) found that hair lichen colonization on second-year twigs declines rapidly with increasing distance from mature timber. Colonization rates decreased to about 50% of maximum at 100 m from the forest edge, then to 10-15% at 300-400 m, and finally to less than 5% beyond 450 m. Based on these findings, Stevenson concluded that dispersal limitations can delay lichen development in young forests. Dettki (1998) and Dettki et al. (2000), working in older forests in Sweden, arrived at a similar conclusion.

The above studies notwithstanding, it can be argued that rates of hair lichen dispersal into young stands are unlikely to affect lichen biomass in the same stands many decades later. As young, regenerating forests develop, tree branches initially exposed to open conditions are increasingly sheltered from ventilation (Oliver and Larson 1996). The corresponding increase in ambient humidity entrains a gradual decline in hair lichen abundance (Goward 1998). Only much later, as stand thinning gives rise to a more open canopy structure, do hair lichens once again prosper in the lower canopy. By that time, however, the upper forest canopy acts as a prominent source of hair lichen diaspores (Goward, in preparation).

The oldgrowth ESSF forests of British Columbia are currently undergoing severe fragmentation due to industrial-scale forestry. Earlier studies on hair lichen reproduction suggest that dispersal limitations in *Alectoria and Bryoria* could impose significant constraints on their ability to colonize the resulting plantation stands (see Dettki et al. 2000). Given the importance of hair lichens in the winter ecology of Mountain Caribou, it would be useful to determine to what extent dispersal is likely to be limiting under these conditions. The primary objective of this study is to report on recent findings pertaining to this question. Special emphasis will be placed on those hair lichen species assumed to provide significant winter forage for Caribou.

Hair Lichens as Forage for Wintering Caribou in ESSF Forests

Little information is available concerning the differential use of hair lichen species by foraging caribou. That some species, however, are less important than others is well documented. Tracking studies by Rominger et al. (1996, 2000) have shown that *Alectoria sarmentosa* is generally not consumed by caribou, except in late autumn, when other food sources are scarce. Possibly this can be accounted for by the relatively low crude protein levels characteristic of this species (Antifeau 1987; Rominger et al. 1996).

Several other hair lichens can probably also be discounted as key forage species for caribou. *Bryoria capillaris, B. implexa, B. lanestris,* and *B. simplicior,* for example, are all rather sparse in the ESSF (Goward and Ahti 1992) and are therefore unlikely to be consumed in quantity. Also infrequent is *Bryoria tortuosa* which, in addition, may be unpalatable owing to high concentrations of vulpinic acid (Brodo and Hawksworth 1977). *Bryoria chalybeiformis* and *Nodobryoria abbreviata,* while slighty more common, are small species restricted in the ESSF to the upper canopy.

Five hair lichen species are much more widely available. Two of these, *B. fuscescens* and *B. glabra,* are most common in rather poorly ventilated sites, usually in the lower canopy (Goward and Campbell, in preparation). These species bear copious tiny powdery outgrowths called soredia. When dislodged, soredia act as asexual reproductive propagules apparently highly efficient at dispersal (Bailey 1976).

Of the remaining species, *Bryoria pseudofuscescens* and *Nodobryoria oregana* lack soredia, whereas *B. fremontii* occasionally produces them, albeit rarely at upper forested elevations (Goward, unpublished observations). These species are most abundant in well-ventilated habitats, especially the

crowns of old trees, where *B. fremontii* and *B. pseudofuscescens* often accumulate to exceptionally heavy loadings. In the lower canopy, they are usually much less prolific, being subject to periodic die-backs (Goward 1998; Goward and Campbell, in preparation). Only in highly exposed sites does the lower canopy support these species in abundance; such sites are highly sought after by foraging caribou (Rominger et al. 1996).

Study Area And Methods

The field portion of this study was conducted at 1850 m in the upper "parkland" forests of Wells Gray Provincial Park (52°N, 120°W). The area is known locally as "Fight Lake Meadow": a shallow, flat-bottomed basin roughly 1 km (east-west) by 2 km (north-south), and surrounded by forested slopes supporting *Abies lasiocarpa* and *Picea engelmannii*. Bioclimatically, Fight Lake Meadow belongs in the orohemiarctic subzone of Tuhkanen (1984) and in the Engelmann Spruce — Subalpine Fir Zone of Meidinger and Pojar (1991). For a more complete description, see Hämet-Ahti (1978) and Goward and Hickson (1995).

In 1996, a two-metre snowpack had accumulated on Fight Lake Meadow by early April. On the morning of 7 April, the surface of the snowpack was covered by a 5 cm layer of fresh snow. A strong southeast wind arose later in the day, accompanied by thawing temperatures. The wind persisted for approximately 18 hours, causing the snow to settle.

After the wind had abated, copious hair lichen fragments could be observed scattered over the surface of the snow. As these fragments appeared to be nonrandomly distributed, a plot study was conducted to examine their spatial distribution. Three 10 m × 10 m plots were established along a north-south transect running the length of the meadow. The first plot was located 100 m from the south end of the meadow, close to the presumed source of the hair lichen fragments. The second plot was established in the centre of the meadow, approximately 1 km north of the first plot. The third plot was situated near the northern end of the meadow, approximately 100 m from the forest edge. Within each of these plots, ten 1 m × 1 m quadrats were established. The position of each quadrat was pre-assigned using two series of randomly generated single-digit numbers. The first series determined the y axis on a cartesian grid, while the second series provided the x axis.

Within each quadrat, a careful enumeration was made of hair lichen fragments larger than about 3 mm. For convenience, dark fragments were recorded as *"Bryoria"*, notwithstanding the additional presence of *Nodobryoria*. Pale greenish fragments of *Alectoria sarmentosa* were also searched for. Within each plot, an attempt was made to identify the largest hair lichen fragments. The presence of nonsorediate hair lichens — *B. fremontii, B. pseudofuscescens,* and *N. oregana* — was especially noted. Also recorded was the number of conifer seeds occurring in each plot.

Results

The data are summarized in Table 1. The plot located closest to the presumed fragment source yielded 2371 *Bryoria* fragments. By contrast, the intermediate plot had 721 fragments, while the plot near the northern edge of the meadow had only 445 fragments. Thus the total number of *Bryoria* fragments observed during this study was 3537. Proportionately few of these appeared to be sorediate, though only the larger thalli could be assessed for soredia. Only one fragment of *Alectoria sarmentosa* was detected.

The largest *Bryoria* fragments noted in each of the plots were 38 cm, 8 cm, and 6 cm long in the southern, intermediate, and northern plots, respectively. Nonsorediate thalli identifiable as *B. "fremontii"* (presumably including *B. pseudofuscescens*) and *Nodobryoria oregana* were observed throughout.

Conifer seeds followed a similar trend, with 23 noted in the southern plot, four in the intermediate plot, and none in the northern plot.

Discussion

Successful dispersal by lichen propagules is a four-step process, consisting of liberation, transport, deposition, and establishment (Bailey 1976). This study illustrates the power of a single windstorm to liberate and transport hair lichen fragments across a snow-covered meadow. The results suggest that fragment densities 100 m from the forest edge exceed two million fragments per hectare. Even at a distance of 2 km from the parent stand, densities are still very high, at roughly 400 000 lichen fragments per hectare. Presumably many of the latter fragments could have been carried to even greater distances, were it not for the 2 km limit imposed by the meadow itself. It should be noted that these comments

TABLE 1. Hair lichen fragments over fresh snow in a subalpine meadow at three distances from the forest edge.

QUADRAT	1	2	3	4	5	6	7	8	9	10	Total
0.1 km	237	268	250	232	218	241	225	217	225	258	2371
1.0 km	54	52	64	77	74	80	85	80	67	88	721
2.0 km	35	53	38	35	46	47	53	39	49	50	445

apply predominantly to nonsorediate species of *Bryoria*; very few sorediate thalli were noted, though this could have been an artifact of the small size of the thallus fragments. *Alectoria sarmentosa* was virtually absent from the study plots, suggesting that fragmentation in this species plays a minor role in medium-range dispersal (see also Dettki et al. 2000).

The northern plot was situated only 100 m from the north edge of the meadow, thus raising the possibility that fragment densities on the snow surface could have been affected by proximity to the adjacent forest. Two scenarios can be advanced: first that reduced wind speeds associated with the forest edge led to enhanced fragment deposition; and second, that hair lichens growing in the adjacent forest constituted a secondary source of lichen fragments, i.e., owing to air turbulence at the forest edge. Neither of these scenarios seems likely to apply in the present instance: first because upwind air flow should be affected to a distance of only three tree lengths (i.e., 50-60 m) from the forest edge (Oke 1978), and second because outward air turbulence from the forest edge ought to have resulted in the transport of at least some conifer seeds into this plot. Compare, by contrast, the presence of four seeds in the intermediate plot, and 23 seeds in the southern plot.

It is of course unknown what proportion of the hair lichen fragments liberated over Fight Lake Meadow during a late winter windstorm in 1996 actually became entangled in the branches of conifers. Nor can it be determined what percentage of the entangled fragments later developed into new lichen thalli. The present observations, however, are consistent with the hypothesis that wind dispersal is of central importance to the life history of at least some hair lichen species in the ESSF (see also Esseen 1985). Indeed, in the absence of wind dispersal, it would be difficult to account for the heavy biomass of nonsorediate hair lichens (e.g., *B. fremontii, B. pseudofuscescens,* and *Nodobryoria oregana*) on solitary trees hundreds of metres from the forest edge. Casual observation suggests that hair lichen community structure on such trees is indistinguishable from that on similar trees much closer to the forest (Goward, unpublished data).

Any major wind event is presumably capable of liberating hair lichen thalli in great numbers. Windstorms occur throughout the year in the ESSF, suggesting that the periodic relocation of hair lichen fragments to the branches of trees is probably a year-round phenomenon. Recent studies, however, suggest that the highest wind speeds occur in winter (Campbell and Coxson 2001), when surface irregularities are covered by snow; this is likely to enhance the medium-distance transport of *Bryoria* thallus fragments.

In an earlier study in southern Wells Gray Park, Edwards et al. (1960) estimated that oldgrowth ESSF forests support as much as 3300 kg of hair lichen biomass per hectare. The fact that the heaviest loadings develop in highly ventilated sites, usually in the upper canopy (Goward, 2003), is probably causally related to the overwhelming abundance of this genus in oldgrowth forests. The close association of at least the nonsorediate *Bryoria* species with sites promoting optimum conditions for thallus liberation and transport doubtless results in dispersal efficiencies much greater than in lowland regions less exposed to wind. Lesser wind strength could thus partly account for the apparent discrepancies between this study, in which hair lichen fragments are wind-transported at least 2 km, and earlier studies reporting pronounced fragment declines beyond about 100 m from the source area (Stevenson 1988; Dettki 1988; Dettki et al. 2000). Other mechanisms of dispersal are probably of greater importance in the sorediate species *B. fuscescens* and *B. glabra*, which are most abundant in portions of the canopy less exposed to wind.

Acknowledgments

This study forms part of the Sicamous Creek Silvicultural Systems Project. The foregoing observations have been distilled from field studies funded in part by Forest Renewal British Columbia (FRBC) and the British Columbia Ministry of Forests. Additional funding was received through Susan Hall, of Parks Canada. For assistance in the field, I thank Palmer Palmer and Tasche M. Hall. André Arsenault, Stephen Clayden, John Flaa, Susan Hall, Rick Pelletier, Murray Peterson, Carla Rydholm and Ken Wright provided constructive comments on an earlier version of the manuscript. The manuscript has also benefitted from comments by two anonymous reviewers.

Documents Cited (marked * in text).

Thomas, D. C., and **D. R. Gray.** 2001. Updated COSEWIC status report on "forest-dwelling" woodland caribou, *Rangifer tarandus caribou*. Committee on the Status of Endangered Wildlife in Canada. Ottawa, Ontario. Draft report. 115 pages.

Literature Cited

Antifeau, T. D. 1987. The significance of snow and arboreal lichens in Wells Gray Provincial Park with special reference to their importance to mountain caribou (*Rangifer tarandus caribou*) in the North Thompson watershed of British Columbia. M.Sc. thesis, University of British Columbia. 142 pages.

Bailey, R. H. 1976. Ecological aspects of dispersal and establishment in lichens. Pages 295-247 *in* Lichenology: Progress and Problems. *Edited by* D. H. Brown, D. L. Hawksworth, and R. H. Bailey. Academic Press, London.

Brodo, I. M., and **D. L. Hawksworth.** 1977. *Alectoria* and allied genera in North America. Opera Botanica 42: 1–164.

Campbell, J., and **D. S. Coxson.** 2001. Canopy microclimate and arboreal lichen loading in subalpine spruce-fir forest. Canadian Journal of Botany 79: 537–555.

Dettki, H. 1998. Dispersal of fragments of two pendulous lichen species. Sauteria 9: 123–132.

Dettki, H., P. Klintberg, and **P.-A. Esseen.** 2000. Are epiphytic lichens in young forests limited by local dispersal? Ecoscience 7: 317–325.

Edwards, R. Y., and **R. W. Ritcey.** 1960. Foods of caribou in Wells Gray Park, British Columbia. Canadian Field-Naturalist 74: 3–7.

Edwards, R. Y., J. Soos, and **R. W. Ritcey.** 1960. Quantitative observations on epidendric lichens used as food by caribou. Ecology 41: 425–431.

Esseen, P.-A. 1985. Litterfall of epiphytic macrolichens in two old *Picea abies* forests in Sweden. Canadian Journal of Botany 63: 980–987.

Esseen, P.-A., K.-E. Renhorn, and **R. B. Pettersson.** 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. Ecological Applications 6: 228–238.

Goward, T. 1998. Observations on the ecology of the lichen genus *Bryoria* in high-elevation conifer forests. Canadian Field-Naturalist 112: 496-501.

Goward, T. 2003. On the vertical zonation of hair lichens (*Bryoria*) in the canopies of high-elevation oldgrowth conifer forests. Canadian Field-Naturalist 117(1): 39–43.

Goward, T., and **T. Ahti.** 1992. Macrolichens and their zonal distribution in Wells Gray Provincial Park and its vicinity, British Columbia, Canada. Acta Botanica Fennica 147: 1–60.

Goward, T., and **A. Arsenault.** 2003. Notes on the *Populus* "dripzone effect" on lichens in well-ventilated stands in east-central British Columbia. Canadian Field-Naturalist 117(1): 61-65.

Goward, T., and **C. Hickson.** 1995. Nature Wells Gray. Lone Pine Publishing, Edmonton. 219 pages.

Hämet-Ahti, L. 1978. Timberline meadows in Wells Gray Park, British Columbia, and their comparative geobotanical interpretation. Syesis 11: 187–211.

McCune, B. 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. Bryologist 96: 405–411.

McCune, B., C. C. Derr, P. S. Muir, A. Shirazi, S. C. Sillett, and **W. J. Daly.** 1996. Lichen pendants for transplant and growth experiments. Lichenologist 38: 161–169.

Meidinger, D., and **J. Pojar.** 1991. Ecosystems of British Columbia. British Columbia Ministry of Forests. 330 pages.

Oke, T. R. 1978. Boundary Layer climates. Methuen & Co. Ltd., New York, New York. 372 pages.

Oliver, C. D., and **B. C. Larson.** 1996. Forest stand dynamics. John Wiley and Sons, New York, New York. 520 pages.

Paquet, M. M. 1997. Toward a mountain caribou management strategy for British Columbia. Background Report. Wildlife Branch, British Columbia Ministry of Environment, Lands and Parks. Victoria. 72 pages.

Peterson, E. B., and **B. McCune.** 2001. Diversity and succession of epiphytic macrolichen communities in low-elevation managed conifer forests in western Oregon. Journal of Vegetation Science 12: 511–524.

Rominger, E. M., C. T. Robbins, and **M. A. Evans.** 1996. Winter foraging ecology of woodland caribou in northeastern Washington. Journal of Wildlife Management 60: 710–728.

Rominger, E. M., C. T. Robbins, M. A. Evans, and **D. J. Pierce.** 2000. Autumn foraging dynamics of woodland caribou in experimentally manipulated habitats, northeastern Washington, USA. Journal of Wildlife Management 64: 160–167.

Stevenson, S. K. 1979. Effects of selective logging on arboreal lichens used by Selkirk caribou. Fish and Wildlife Report R-2. British Columbia Ministry of Forests, Victoria, British Columbia. 76 pages.

Stevenson, S. K. 1988. Dispersal and colonization of arboreal forage lichens in young forests. British Columbia Ministry of Environment and British Columbia Ministry of Forests, IWIRF (Integrated Wildlife Intensive Forestry Research) 38. Victoria, British Columbia.

Tuhkanen, S. 1984. A circumboreal system of climatic-phytogeographical regions. Acta Botanica Fennica 127: 1–50.

Received 1 November 2000
Accepted 9 May 2003

Sympatric Presence of Low and High Gillraker Forms of Cisco, *Coregonus artedi*, in Lake Athapapuskow, Manitoba

KATHERINE A. A. AOKI and R. A. BODALY[1]

[1]Freshwater Institute, Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, Manitoba R3T 2N6 Canada

Aoki, Katherine A. A., and R. A. Bodaly. 2003. Sympatric presence of low and high gillraker forms of Cisco, *Coregonus artedi*, in Lake Athapapuskow, Manitoba. Canadian Field-Naturalist 117(1): 49–52.

Cisco-like fishes caught in Lake Athapapuskow were all Cisco, *Coregonus artedi,* but showed a bimodal gillraker distribution with modes at 38/39 and 44/45 gillrakers. Low gillraker fish were smaller and had more lightly pigmented pectoral fins as compared to high gillraker fish. Gillraker length did not differ between the two forms. Most fish caught in deep water (38 m) were the low gillraker form whereas approximately equal numbers of the two forms were caught in shallower water (15-25 m). We conclude that there are two forms of Cisco in Lake Athapapuskow. The Shortjaw Cisco, *C. zenithicus*, was not caught in the lake, although an earlier report had documented its presence.

Key Words: Cisco, *Coregonus artedi*, Lake Athapapuskow, Manitoba, Canada, sympatric forms, gillraker, colouration

There are many reports of sympatric forms of coregonid fishes throughout their distribution (e.g., Clarke 1973; Turgeon et al. 1999; Vuorinen et al. 1993). Instances of closely related populations living sympatrically in a lake are of great importance in the study of evolutionary mechanisms and ecological theory. The best available models to study the behavioural, ecological, and genetic changes that may occur during species formation are sympatric occurrences of closely related forms of fish (Skulason and Smith 1995).

The ciscoes belong to the genus *Coregonus* and have generally terminal mouths, a large number of gillrakers, relatively small size and planktivorous feeding habits. (Here we use the term "cisco" to refer to all cisco-like fishes and the term "Cisco" to refer to the species *C. artedi.*) As for other coregonids, closely-related sympatric forms of ciscoes are known in various locations in North America. In the Laurentian Great Lakes and Lake Nipigon, numerous species exist (or existed) that are probably derived post-glacially from colonising forms related to two presumably original cisco species, the Cisco (*C. artedi*) and the Shortjaw Cisco (*C. zenithicus*) (Todd and Smith 1992; Turgeon et al. 1999). Outside the Great Lakes, cisco taxonomy has been little studied. Henault and Fortin (1989) reported a spring spawning form of Cisco that coexisted with fall spawning Cisco in a Quebec lake. Clarke (1973) reported a number of cases of sympatric forms of Cisco in Canada and also lakes in which Cisco were sympatric with Shortjaw Cisco. Clarke's findings included Lake Athapauskow, where he reported three kinds of ciscoes, Shortjaw Cisco and two forms of Cisco that differed in gillraker counts.

The purpose of this study was to characterize the cisco fauna of Lake Athapapuskow, Manitoba to confirm the existence of sympatric forms of ciscoes in the lake.

Lake Athapapuskow is a large (surface area 270.3 km^2), deep lake, located in west-central Manitoba on the Precambrian shield. The lake was fished in September 1997 using experimental gillnets with panels of mesh sizes from 1.5 – 13.3 cm stretched measure. Net 1 was set approximately 38 m deep at 54° 37′ 33" N; 101° 39′ 06" W. Net 2 was placed at a shallower location at depths from 15 – 26 m at 54° 37′ 53"; 101° 37′ 37" W. A total of 230 ciscoes (Cisco, *C. artedi,* and/or Shortjaw Cisco, *C. zenithicus*) were captured and examined for species characteristics. All fish were determined to be Cisco and not Shortjaw Cisco because all had terminal or supra-terminal mouths, premaxillae not making an angle in snout profile, short maxillae not extending to middle of eye, and a large number of gillrakers (minimum 35) (Clarke 1973; Scott and Crossman 1973; K. W. Stewart, Department of Zoology, University of Manitoba, unpublished manuscript: Keys to the freshwater fishes of Manitoba with some species added from adjacent areas). A sample of 55 fish was examined in detail. Weight (+/- 1 g), fork length (+/- 1 mm) were determined. Eye diameter and gillraker length were measured using dial calipers (+/- 0.1 mm) following Hubbs and Lagler (1964). Fish were sexed internally and the state of maturity was estimated by visual examination. Fish were judged to be mature if they were going to spawn in the year of capture. Gillraker number was counted on the first arch, generally on the left side, under a dissecting microscope. Mouth position was scored as lower jaw longer than upper jaw or jaws of equal length. Pectoral fin colouration was scored as immaculate, or slight, moderate, or strong pigmentation on the dorsal margin.

The frequency distribution of total gillraker number for Cisco in Lake Athapapuskow was bimodal (Figure 1). Modes were evident at 38/39 and 44/45 gillrakers. On the basis of gillraker number, fish

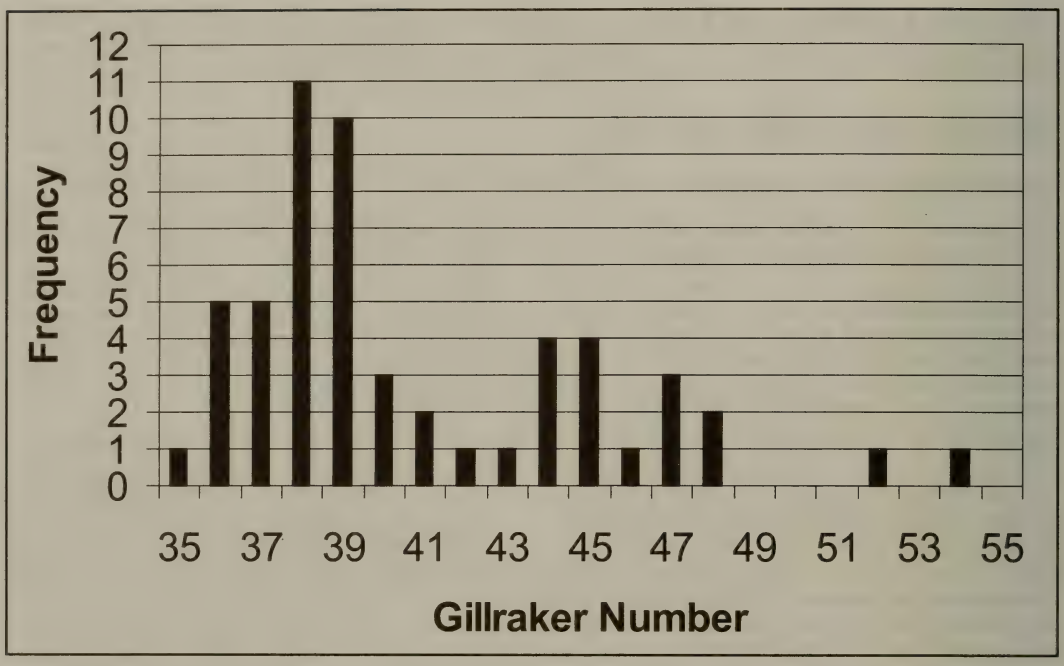


FIGURE 1. Distribution of total gillraker number in ciscoes from Lake Athapapuskow, caught September 1997.

were separated into two groups, low and high gillraker. Fish with 42 or 43 gillrakers were not classified due to uncertainty regarding their type because they were intermediate between the low and high gillraker fish, Low gillraker fish were smaller (mean fork length 142 mm; range 105 – 165 mm) than high gillraker fish (mean 189 mm; range 150-255 mm). Gillraker length was shorter for low gillraker fish but the relationship between gillraker length and fork length was similar for the two groups (Figure 2). All fish (except one) of both groups had a longer lower jaw than upper jaw. Almost all fish of both groups (86% of lowraker and 93% of highraker fish) were mature and probably would have spawned in the year of capture. High gillraker fish had more heavily pigmented pectoral fins as compared to low gillraker fish. Twenty-one of 37 (57%) of low gillraker fish had immaculate pectoral fins whereas the fins of all high gillraker fish showed at least some pigmentation. Low gillraker fish had larger eyes, relative to fish length, than high gillraker fish (Figure 3). In the length range for which there was overlap of the sizes of the two forms (150-165 mm), low gillraker fish had a mean eye diameter of 9.4 mm (range 7.7-10.6 mm) whereas high gillraker fish had a mean eye diameter of 8.4 mm (range 6.9-9.4 mm). High gillraker fish inhabited shallower depths in the lake, at least during September when fishing was conducted. Of 20 fish examined from the deeper net (38 m), 18 were low gillraker fish. Of 33 fish examined from the shallower net (15-26 m), 19 were low gillraker fish and 14 were high gillraker fish. Both fish with intermediate gillraker counts (42 and 43) and both fish with extreme counts (52 and 54) had pigmented pectoral fins and were caught in the shallower net, indicating that they probably were high gillraker fish.

Our results suggest that there are two forms of Cisco existing sympatrically in Lake Athapapuskow. This conclusion is supported by morphological and meristic differences between the two forms, including gillraker number, size, fin colouration, and eye diameter. The two Cisco forms also differed in their depth distributions in the lake in September and almost all fish of both forms were mature, excluding the possibility that the smaller fish were immature members of the same population as the large fish. Our results differ from those of Clarke (1973), who found two forms of Cisco with modal gillraker counts of 43 (mean 42.3; range 38-47) and 48 (mean 45.6; range 42-49), plus Shortjaw Cisco with a modal gillraker count of 32 (mean 29.4; range 24-36). Shortjaw Cisco either no longer exist in the lake, or were not captured by the sampling for this study. The latter appears most likely as Shortjaw Cisco may have been in deeper waters that were not sampled. The gillraker counts of the two Cisco forms caught in 1997 differ noticeably from those of fish caught 30 years earlier in the late 1960s although all of the gillrakers counted by Clarke (1973) are within the range found in this study. The differences could be due to counting

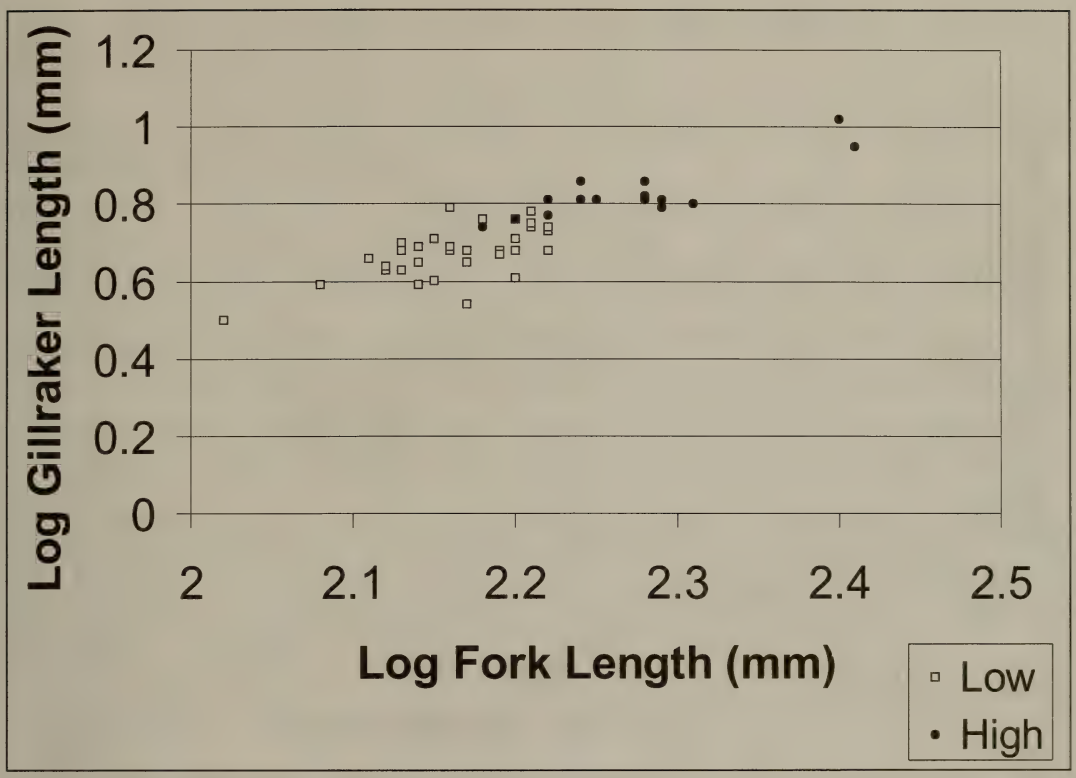


FIGURE 2. Relationship between gillraker length and fork length for low and high gillraker ciscoes from Lake Athapapuskow.

technique or to actual changes in gillraker numbers over the 30-year interval between sampling.

The primary debates regarding the origin of closely related sympatric forms of coregonid fishes centre on timing (post-glacial vs. glacial) and mechanism (sympatric vs. geographic) of speciation. Many recent authors have tended to favour a post-glacial, sympatric origin for these forms (e.g., Clarke 1973; Todd and Smith 1992; Turgeon et al. 1999). Schluter (1996) has emphasized the role of resource-driven selection pressures and competition for resources in producing reproductive isolation within lakes. Successive waves of invading populations during post-glacial colonization of lakes may also have provided the opportunity for microgeographic speciation.

Two questions remain regarding the ciscoes of Lake Athapapuskow. First, has the Shortjaw Cisco disappeared from the lake? Further sampling is needed at greater depths. Second, are the two forms of Cisco completely reproductively isolated in the lake? The existence of reproductive isolation between the sympatric ecotypes will require more intensive work on the timing and location of spawning and also on the genetic relationship between the two forms.

Acknowledgments

We thank Robert Fudge and James Johnson for capturing the fish and James Reist and Robert Fudge for assistance in the lab. Thanks also to Mme. Radi for valuable advice.

Literature Cited

Clarke, R. M. 1973. The systematics of ciscoes (Coregonidae) in central Canada. Ph.D. thesis, University of Manitoba, Winnipeg, Manitoba.

Henault, M., and **R. Fortin.** 1989. Comparison of meristic and morphometric characters among spring- and fall-spawning ecotypes of cisco (*Coregonus artedii*) in southern Quebec, Canada. Canadian Journal of Fisheries and Aquatic Sciences 46: 166–173.

Hubbs, C. L., and **K. F. Lagler.** 1964. Fishes of the Great Lakes region. University of Michigan Press, Ann Arbor.

Scott, W. B., and **E. J. Crossman.** 1973. Freshwater Fishes of Canada. Bulletin of the Fisheries Research Board of Canada 184.

Skulason, S., and **T. B. Smith.** 1995. Resource polymorphisms in vertebrates. Trends in Ecology and Evolution 10: 366–370.

Schluter, D. 1996. Ecological causes of adaptive radiation. American Naturalist 148: 540–564.

Todd, T. N., and **G. R. Smith.** 1992. A review of differentiation in Great Lakes ciscoes. Polish Archives of Hydrobiology 39: 261–267.

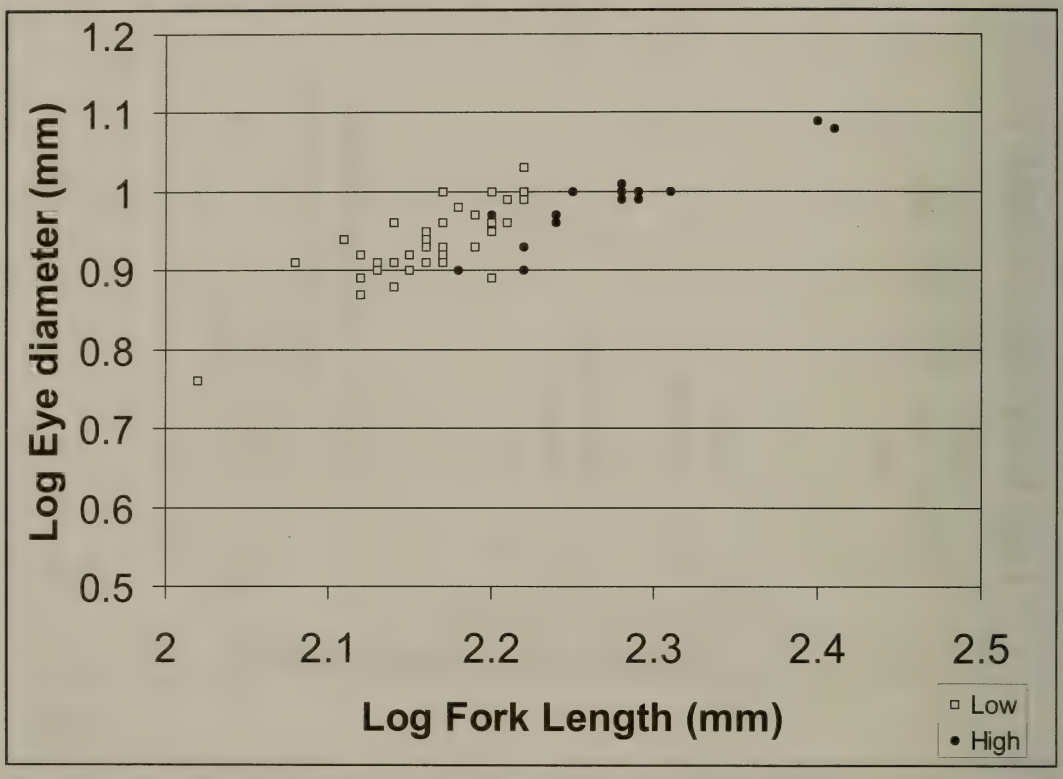


FIGURE 3. Relationship between eye diameter and fork length for low and high gillraker ciscoes from Lake Athapapuskow.

Turgeon, J., A. Estoup, and **L. Bernatchez.** 1999. Species flock in the North American great lakes: Molecular ecology of Lake Nipigon ciscoes (Teleostei: Coregonidae: *Coregonus*). Evolution 53: 1857–1871.

Vuorinen, J., R. A. Bodaly, J. D. Reist, L. Bernatchez, and **J. J. Dodson.** 1993. Genetic and morphological differentiation between dwarf and normal size forms of lake whitefish (*Coregonus clupeaformis*) in Como Lake, Ontario. Canadian Journal of Fisheries and Aquatic Sciences 50: 210-216.

Received 11 December 2000
Accepted 29 May 2003

Sightings of Vagrant Pacific Alcids in Desolation Sound, British Columbia

Laura McFarlane Tranquilla[1,2], Falk Huettmann[3], Cecilia Lougheed[4], Lynn Lougheed[5], Nadine Parker[1], and Gary Kaiser[6]

[1]Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6 Canada
[2]Corresponding author: Email: lat@sfu.ca
[3]Current address: Geography and Earth Sciences Department, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2N 1N4 Canada
[4]Current address: Canadian Wildlife Service, Environment Canada, Ottawa, Ontario K1A 0H3 Canada
[5]Current address: 18 Rupert Street, Ottawa, Ontario K1S 3S3 Canada
[6]Current address: Nature Conservancy of Canada, 202-26 Bastions Square, Victoria, British Columbia, V8W 1H9 Canada

Tranquilla, Laura McFarlane, Falk Huettmann, Cecilia Lougheed, Lynn Lougheed, Nadine Parker, and Gary Kaiser. 2003. Sightings of vagrant Pacific alcids in Desolation Sound, British Columbia. Canadian Field-Naturalist 117(1): 53–56.

From May through August during each year from 1997 through 2000, we conducted repeated daytime and nighttime boat surveys, in Desolation Sound, at the north end of the Strait of Georgia, British Columbia, Canada. During the four study years, we captured 1184 Marbled Murrelets and sighted 14 161 more. During the same period, we recorded seven other alcids considered rare in the study area: two Ancient Murrelets (*Synthliboramphus antiquus*), one Parakeet Auklet (*Cyclorhynchus psittacula*), and four Rhinoceros Auklets (*Cerorhinca monocerata*). In light of our intensive search effort in the study area, our results confirm scarcity relevant to summer distribution patterns of Pacific alcids.

Key Words: Marbled Murrelet, *Brachyramphus marmoratus,* Ancient Murrelet, *Synthliboramphus antiquus*, Parakeet Auklet, *Cyclorhynchus psittacula*, Rhinoceros Auklet, *Cerorhinca monocerata*, coastal waters, Desolation Sound, British Columbia, at-sea surveys, dipnetting.

Desolation Sound, British Columbia, and the adjoining Malaspina, Lancelot, Okeover, and Theodosia Inlets (Figure 1) are relatively productive marine areas. Moderate tidal currents flow into the inlets, and during the summer dense schools of sand lance (*Ammodytes hexapterus*) are observed in Malaspina Inlet and Desolation Sound (Kaiser et al. 1991*). The study area attracts a dense population of Marbled Murrelets (*Brachyramphus marmoratus*) during the breeding season (Kaiser et al. 1991*; Derocher et al. 1996*), and Pigeon Guillemots breed near the Sound on Mitlenatch Island. A number of other marine-feeding birds are commonly seen in Desolation Sound and adjacent inlets (e.g., Glaucous-winged, Mew, and Bonaparte's gulls, and Surf Scoters) (Mahon et al. 1992). During the summers of 1997-2001, Desolation Sound was the site of a demographic and radio-tracking study of Marbled Murrelets (Cooke 1999; Centre for Wildlife Ecology, Simon Fraser University, unpublished data). Throughout this study, the coastal area was intensively surveyed for murrelets, with an almost 24-hour coverage, allowing observation of many bird species that might appear in the study area. Here we report scarcity data for three alcid species rare in Desolation Sound.

*See Documents Cited section

Methods

We surveyed Desolation Sound (50° 05'N, 124° 40'W) and adjacent Theodosia, Lancelot, Okeover, and Malaspina inlets for birds using two techniques, each designed for different purposes (Lougheed et al. 1998*). Firstly, daytime at-sea surveys (Table 1) were conducted from April through August during 1997 – 1999, following pre-defined waypoints on a hand-held GPS (Global Positioning Systems) (see more details in Lougheed et al. 2002). From April to September 2000, DISTANCE sampling methodology (Buckland et al. 1993) was employed along the same transect waypoints. One driver and two observers, some of whom remained consistent across years, conducted the surveys. In general, the sea surface was scanned for seabirds with the naked eye, and positive identification was made using binoculars. In 1997, when 24-hour Marbled Murrelet telemetry was done for most of the field season, the study area was also opportunistically scanned daily for seabirds (Lougheed et al. 1998*). Secondly, the study area was surveyed during nighttime capture sessions every night (ca. 22:00 – 06:00), weather permitting, throughout the breeding season each summer (Table 1). These searches were done to catch murrelets using the "dipnetting" technique (Whitworth et al. 1997; Vanderkist et al. 2000), using two 4.5 m inflatable boats, with three or four people in each boat using high-powered spotlights to

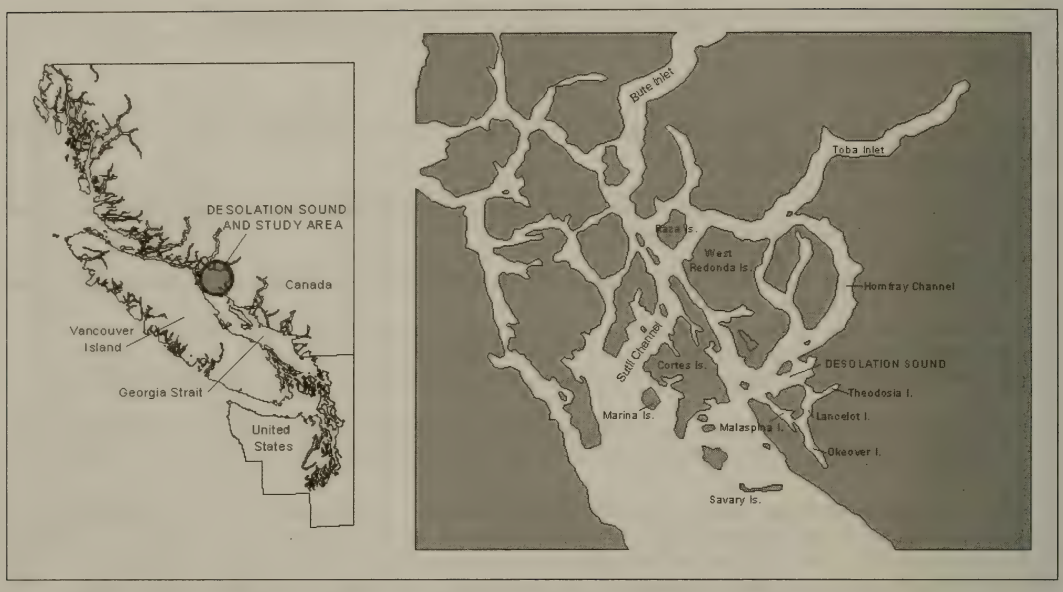


FIGURE 1. Desolation Sound, British Columbia, and adjacent inlets (Malaspina, Okeover, Lancelot, Theodosia) included in the study area.

search the surface of the water. Birds seen in the spotlight were approached stealthily, as closely as possible, and scooped from the surface of the water with a salmon landing net. This close approach allowed identification of birds not captured.

Results

A total of 337 nights on the water, averaging 6 hours per night, and 58 daytime at-sea surveys were conducted during the four study summers (Table 1). During these four years, we captured 1184 Marbled Murrelets and sighted 14 161 more on at-sea surveys (Centre for Wildlife Ecology, Simon Fraser University, unpublished data). Although not quantified here, Pigeon Guillemots (*Cepphus columba*) were somewhat common in the area, with a few pairs observed in Malaspina Inlet every year during at-sea surveys, and some breeding near the study area on Mitlenatch Island. We made seven observations of three alcid species rare to the study area (Table 2):

TABLE 1. Nocturnal search effort (dipnetting) and daytime at-sea survey effort in Desolation Sound from 1997 to 2000.

Year	Number of nights dipnetting	Number of daytime at-sea surveys
1997	70	23
1998	74	17
1999	97	9
2000	96	9
Total	337	58

(1) **Parakeet Auklet.** One Parakeet Auklet was captured on 13 March 1998, measured, photographed, but not banded.

(2) **Ancient Murrelets.** One Ancient Murrelet was captured during a dipnet session on 6 August 1999, caught, banded, measured, and photographed (band and photograph available on request). One Ancient Murrelet was seen during a dipnet session on 20 July 2000. Neither Ancient Murrelet had plumage characteristics of breeding adults, and thus, were suspected juveniles or non-breeders.

(3) **Rhinoceros Auklets.** One Rhinoceros Auklet was seen during a dipnet session on 16 May 1997, and another Rhinoceros Auklet was seen during a daytime at-sea survey on 8 June 1999. The lack of plumes and appearance of the bill suggested that this second one was a non-breeding sub-adult. Two sub-adult Rhinoceros Auklets were caught during dipnet sessions on 14 August 2000 and 20 August 2000.

Discussion

Marbled Murrelets are widespread and fairly abundant in the coastal waters of British Columbia (Rodway et al. 1992; Campbell et al. 1990; Kaiser et al. 1991*). This environment offers foraging opportunities close to their inland breeding habitat in coastal old-growth forests (Nelson 1997). In contrast, Ancient Murrelets, Rhinoceros Auklets, and Parakeet Auklets are seen rather rarely on the inner and south coasts of British Columbia (see review of species' distributions in Campbell et al. 1990). Six of seven of our "rare alcid" observations were made

TABLE 2. Seven vagrant alcids sighted during the summers of 1997-2000 in Desolation Sound, British Columbia. RHAU = Rhinoceros Auklet, PAAU = Parakeet Auklet, ANMU = Ancient Murrelet. "Dipnet" method occurred at night, while "survey" method occurred during the day.

Species	Method	Date	Capture or Sighting	Time (PST)	Comments	Location description
RHAU	dipnet	16 May 1997	sighting	00:30	breeding plumage	Middle of Desolation Sound
PAAU	dipnet	13 March 1998	capture	21:19	na	Near SW Zephine Head, Desolation Sound
RHAU	survey	8 June 1999	sighting	10:00	Suspected juvenile (based on plumage)	Between Mink Island and Galley Bay, Desolation Sound
ANMU	dipnet	6 August 1999	capture	04:44	Immature or non-breeding plumage	Near East Redonda, mouth of Homfray Channel
ANMU	dipnet	20 July 2000	sighting	04:01	Immature or non-breeding plumage	Near mouth of Homfray Channel
RHAU	dipnet	14 August 2000	capture	04:00	Juvenile plumage	Southeast tip of Mink Island, Desolation Sound
RHAU	dipnet	21 August 2000	capture	01:00	Juvenile plumage	Near Kinghorn Island, Desolation Sound

during nighttime work, suggesting that nocturnal movements may be an important feature of alcid dispersal or migration.

While it has been suggested that Parakeet Auklets might be a regular winter visitor in offshore waters of British Columbia, nearshore sightings are rare (Campbell et al. 1990; Gaston and Jones 1998). They were unrecorded until six oiled carcasses washed ashore near Tofino after the Nestucca oil spill of 1989 (Campbell et al. 1990).

Hundreds of Rhinoceros Auklets use the protected waters north and south of the Strait of Georgia, and large flocks of Ancient Murrelets winter near the south end (Campbell et al. 1990). However, there are no breeding colonies of these alcids within the Strait of Georgia, suggesting that each species is unable to exploit the resources of the Strait itself. Although as many as 27 Rhinoceros Auklets have been seen off Mitlenatch Island on summer evenings, breeding there has not been confirmed. Large numbers forage in tidal rapids throughout the Broughton Archipelago, north of the study site, and one or two are often seen during winter seabird surveys that pass through Desolation Sound (G. Kaiser, unpublished data). Several thousand breed on Protection Island, Washington, at the south end of the Strait of Georgia and may have been the source of the captured sub-adult birds. In spite of these nearby concentrations, surprisingly few birds were seen in the Desolation Sound area.

During the summer Ancient Murrelets are common along the northern mainland coast, and have been recorded near Desolation Sound in winter (Mitlenatch Island, Sechelt, and Sunshine Coast), but appear to avoid coastal inlets and fjords unless a storm occurs. Ancient Murrelets frequently feed in channels with strong currents and tidal flow. Desolation Sound would seem to be such a location; its inlets and fjords often have moderately strong tidal eddies and currents (Derocher et al. 1996*), which attract more dense groups of Marbled Murrelets than elsewhere in the study area. However, the resources available here are apparently not used by Ancient Murrelets.

Our work provides important and confirmed scarcity data relevant for species distribution patterns of Parakeet Auklets, Ancient Murrelets, and Rhinoceros Auklets. In spite of an intensive search effort over four years, day and night, it appears that alcid species other than Marbled Murrelets and Pigeon Guillemots in Desolation Sound are truly rare. This suggests that, although apparently productive, Desolation Sound may not provide suitable marine habitat for other auks. The distribution of rare species in Desolation Sound may also be affected by sea-surface temperature and salinity, both of which are influenced by the influx of freshwater (from estuaries and snow- or glacial-runoff) to the area (Kaiser et al. 1991*), as well as by turbidity of the inlets. These conditions may influence prey distribution and/or foraging efficiency. In spite of suitable foraging conditions for Marbled Murrelets in Desolation Sound, it may be that Desolation Sound is too far from other alcids' breeding colonies, or may be too far out of their observed winter ranges. It may also be significant that the numerous mixed-species feeding flocks reported by Mahon et al. (1992) have not been observed since; perhaps resources are too unpredictable for most fish-eating birds. Overall, our findings are in agreement with

reports of distribution ranges for these species (Gaston and Jones 1998; Campbell et al. 1990; Morgan et al. 1993*), and provide important species scarcity information for Desolation Sound, in light of long-term baseline information for coastal British Columbia.

Acknowledgments

We owe all of our data to the tremendous efforts of field crews who worked with us day and night on this project. Thanks to Connie Smith for assistance obtaining banding permits, and to Fred Cooke, the Centre for Wildlife Ecology at Simon Fraser University and the Canadian Wildlife Service, for logistical support. Fred Cooke and two anonymous reviewers made valuable comments on drafts of the manuscript. This project was funded by Forest Renewal British Columbia, National Sciences and Engineering Research Council of Canada, Centre for Wildlife Ecology at Simon Fraser University, Canadian Wildlife Service, British Columbia Ministry of Forests, the Science Council of British Columbia, Timber-West Forest Ltd., International Forest Products Ltd., Western Forest Products Ltd., Weyerhauser International, National Council for Air and Stream Improvement, and Pacific Forest Products Ltd.

Documents Cited (marked * in text)

Derocher, A., G. Kaiser, F. Cooke, I. Manley, and **M. Gill**. 1996. Research on Marbled Murrelets in the Desolation Sound area during the 1994 breeding season. Technical Report Series (257), Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.

Kaiser, G. W., T. E. Mahon, and **M. Fawcett**. 1991. Studies of Marbled Murrelets in marine habitats, during 1990. Technical Report Series (131). Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.

Lougheed, L. W, C. Lougheed, B. A. Vanderkist, S. Webster, R. Bradley, M. Drever, I. Manley, G. W. Kaiser, and **F. Cooke**. 1998. Demography and ecology of Marbled Murrelets in Desolation Sound, British Columbia. Technical Report (004). CWS/NSERC Wildlife Ecology Chair, Simon Fraser University, Burnaby, British Columbia.

Morgan, K. K., R. Vermeer, and **W. McKelvey**. 1993. Atlas of pelagic birds of western Canada. Environment Canada, Canadian Wildlife Service.

Literature Cited

Buckland, S. T., D. R. Anderson, K. P. Burnham, and **J. L. Laake**. 1993. Distance sampling: estimating the abundance of biological populations. Chapman and Hall, London.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. Kaiser, and **M. C. E. McNall.** 1990. The Birds of British Columbia. Royal British Columbia Museum, Environment Canada, Canadian Wildlife Service. Volume 2.

Cooke, F. 1999. Population studies of Marbled Murrelets (*Brachyramphus marmoratus*) in British Columbia. *In* Biology and Conservation of Forest Birds. *Edited by* A. W. Diamond and D. N. Nettleship. Society of Canadian Ornithologists. Special publication (1). Fredericton, New Brunswick.

Gaston, A. J., and **I. L. Jones**. 1998. The Auks. Bird Families of the World. Oxford University Press.

Lougheed, C., L. W. Lougheed, F. Cooke, and **S. Boyd**. 2002. Local survival of adult and juvenile Marbled Murrelets and their importance for estimating reproductive success. Condor 104: 309–318.

Mahon, T. E., G. W. Kaiser, and **A. E. Burger.** 1992. The role of Marbled Murrelets in mixed-species feeding flocks in British Columbia. Wilson Bulletin 104: 738–743.

Nelson, S. K. 1997. Marbled Murrelet, *Brachyramphus marmoratus*. *In* The Birds of North America (276). *Edited by* A. Poole and F. Gills. The Academy of Natural Sciences, Philadelphia, and the American Ornithologists' Union, Washington, D.C.

Rodway, M. S., H. R. Carter, S. G. Sealy, and **R. W. Campbell**. 1992. Status of the Marbled Murrelet in British Columbia. Proceedings of the Western Foundation of Vertebrate Zoology 5: 17–41.

Vanderkist, B. A., T. D. Williams, D. F. Bertram, L. Lougheed, and **J. P. Ryder**. 2000. Indirect, physiological assessment of reproductive state and breeding chronology in free-living birds: an example in the Marbled Murrelet (*Brachyramphus marmoratus*). Functional Ecology 14: 758–765.

Whitworth, D. L., J. Y. Takekawa, H. R. Carter and **W. R. McIver**. 1997. A night-lighting technique for at-sea capture of Xantus's Murrelets. Colonial Waterbirds 20: 525–531.

Received 27 December 2000
Accepted 25 April 2003

Range Extensions of Logperch, *Percina caprodes*, and Longnose Dace, *Rhinichthys cataractae*, in Newfoundland and Labrador

ROBERT PERRY[1] and TAMMY L. JOYCE[2]

[1]Inland Fish Section, Inland Fish and Wildlife Division, Department of Tourism, Culture and Recreation, Post Office Box 2007, Commerce Court, Corner Brook, Newfoundland and Labrador A2H 7S1 Canada

[2]Endangered Species and Biodiversity Section, Inland Fish and Wildlife Division, Department of Tourism, Culture and Recreation, Post Office Box 2007, Commerce Court, Newfoundland and Labrador A2H 7S1 Canada

Perry, Robert, and Tammy L. Joyce. 2003. Range extensions of Logperch, *Percina caprodes*, and Longnose Dace, *Rhinichthys cataractae*, in Newfoundland and Labrador. Canadian Field-Naturalist 117(1): 57–60.

The Logperch, *Percina caprodes*, is reported from a single location in Ashuanipi Lake, Labrador. This is the second record for Labrador. The Longnose Dace, *Rhinichthys cataractae*, is reported from several locations in Lake Shabogamo, Labrador, representing the first report for this lake.

Key Words: Logperch, *Percina caprodes*, Longnose Dace, *Rhinichthys cataractae*, Newfoundland, Labrador, distribution.

Labrador, the continental portion of the Province of Newfoundland and Labrador, comprises a land mass of approximately 293 000 km^2 in the northeastern section of North America. It is an area which remains largely undeveloped, with an estimated population of only 31 000 people (Anderson 1985). The vast majority of Labrador's watersheds and forests remain pristine with virtually no development. Due to this lack of development there has been only a cursory cataloguing of the occurrence and distribution of Labrador's flora and fauna. Reports of fish species in the interior have largely been in environmental impact statements for hydro development. Large areas have not been satisfactorily examined at all.

Labrador Survey

In an effort to manage and understand its freshwater fish stocks better, the Government of Newfoundland and Labrador has begun a sampling program to quantify fish species occurrence, distribution and relative abundance in the southwestern portion of Labrador. The program involves sampling major water bodies in the early spring when lakes are considered to be the same temperature throughout (homothermic). Homothermic conditions are thought to ensure better representation of all species as fish should not be stratified in accordance with their optimal water temperature preferences (Lester et al. 1991).

Logperch

During an experimental gill netting survey of Ashuanipi Lake, a single Logperch, *Percina caprodes,* was captured in the Kapitagas Channel (52° 24.99′ N, 66° 07.92′ W) near the mouth of the Esquimaux River (Figure 1). Ashuanapi Lake flows into the upper Churchill drainage basin, which lies between 53° and 55°N and 63° and 66°W on the Labrador plateau, between 400 and 575 m above sea level. This collection represents the second reported capture of a Logperch within Labrador and the first report for Ashuanapi Lake. Grant et al. (2001) earlier reported a Labrador population of Logperch from Lake Atikonak (Figure 1). The Logperch from Lake Ashuanipi was captured on 14 June 2000 in 1.25 cm mesh in approximately 1 m of water. The bottom substrate was 100% sand, and the surface water temperature was 14.1°C. The net was set for a period of 17 hours. Other species caught in the same net set include: 16 Lake Trout, 1 Brook Trout, 30 Lake Whitefish, 25 Longnose Sucker, 13 White Sucker and 4 Lake Chub (see Table 1 for scientific names).

The captured Logperch (Figure 2) demonstrated body attributes within the normal range for the species. It was orange-green in colour with black bars along the length of its body. The underside was white. The fish measured 77 mm in length and weighed 3.52 g; anterior and posterior dorsal fins had 14 and 16 fin rays, respectively. The left and right pectoral fin each had 14 rays; each pelvic fin had 6 rays. The anal fin had one spine and 10 soft rays. The caudal fin had 20 fin rays. The fish scales were ctenoid.

Scott and Crossman (1973) described the Logperch as a wide-ranging species, occurring from Lac Saint Jean and the St. Lawrence tributaries of Quebec, west to Saskatchewan, north throughout Ontario to Hudson and James Bays and the Churchill River in Manitoba, and south through the Great Lakes and the Mississippi River system to the Rio Grand River of southern Texas. In addition, Power (1965) reported an isolated population in the Aguanus River of eastern Quebec located on the north shore of the Gulf of St. Lawrence. Our capture site is approximately 380 km from the isolated south east location in the Aguanus River, 100 km from the Lake Atikonak location and 550 km from Lac Saint Jean. In total, Black et al. (1986) documented 23

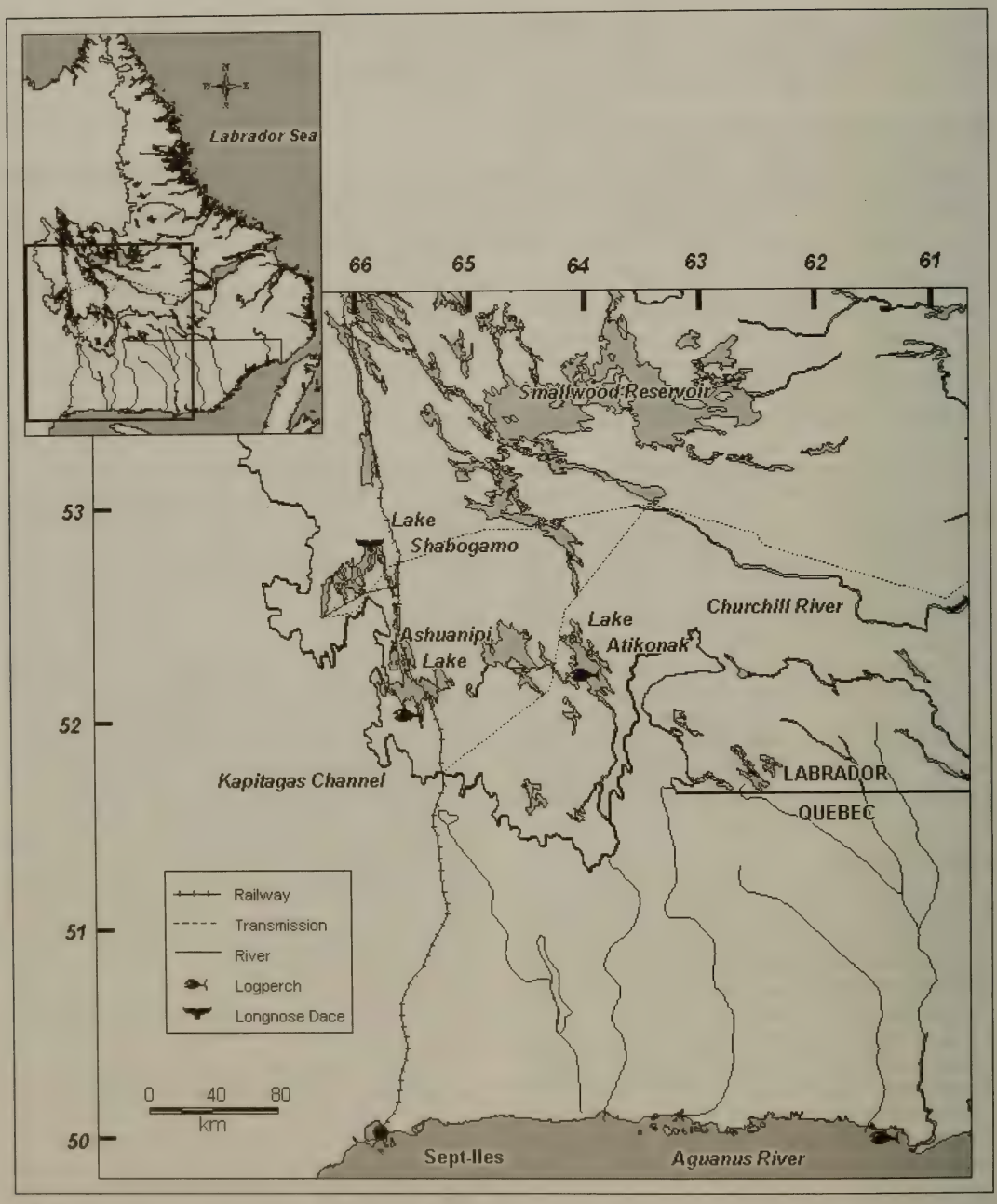


FIGURE 1. Recent discovery locations of the Logperch, *Percina caprodes*, and Longnose Dace, *Rhinichthys cataractae*, in Labrador. The Aguanus River, Quebec, and Ashuanapi Lake and Lake Shabogamo, Labrador, sites are indicated as point locations. (Adapted from Scott and Crossman 1973).

obligate spawners and one catadromous species existing within the boundaries of Labrador. The presence of the Logperch increases the number of reported species for Labrador to 24 obligate spawners and one catadromous species (Table 1).

Longnose Dace

Longnose Dace were collected from two locations in the northeastern portion of Lake Shabogamo (Figure 1). These captures represent the first records of Longnose Dace from Lake Shabogamo and sup-

TABLE 1. List of fish species recorded as being present in Labrador (* Represented by only a few reported occurrences).

Family	Scientific Names	Common Names	Reference
Salmonidae	*Salvelinus fontinalis*	Brook Trout	Weed 1934; Stearns 1883
	Salvelinus namaycush	Lake Trout	Bruce et al. 1979; Weed 1934
	Salvelinus alpinus	Arctic Charr	Scott and Crossman 1973
	Salmo salar	Atlantic Salmon	Stearns 1883
	Prosopium cylindraceum	Round Whitefish	Bruce et al. 1979
	Coregonus clupeaformis	Lake Whitefish	Bruce et al. 1979
	*Oncorhynchus gorbuscha**	Pink Salmon	Dempson 1980; Lear 1975
Osmeridae	*Osmerus mordax*	Rainbow Smelt	Stearns 1883
Esocidae	*Esox lucius*	Northern Pike	Bruce et al. 1979
Cyprinidae	*Couesius plumbeus*	Lake Chub	Backus 1951
	*Semotilus margarita**	Pearl Dace	Scott and Crossman 1973
	Rhinichthys cataractae	Longnose Dace	Ryan 1980
Catastomidae	*Catastomous catostomous*	Longnose Sucker	Scott and Crossman 1973
	Catostomous commersoni	White Sucker	Scott and Crossman 1973
Anguillidae	*Anguilla rostrata*	American Eel	Scott and Scott 1988; Backus 1957
Gadidae	*Lota lota*	Burbot	Black et al. 1986
Gasterosteidae	*Gasterosteus aculeatus*	Threespine Stickleback	Stearns 1883
	Pungitius pungitius	Ninespine Stickleback	Stearns 1883
Cottidae	*Cottus bairdi*	Mottled Sculpin	Black et al. 1986
	Cottus cognatus	Slimy Sculpin	Black et al. 1986
Petromyzontidae	*Petromyzon marinus**	Sea Lamprey	Low 1896; Murphy 1972
Clupeidae	*Alosa pseudoharengus**	Alewife	Backus 1957
	*Alosa sapidissima**	American Shad	Hare and Murphy 1974
Acipenseridae	*Acipenser oxyrynchus**	Atlantic Sturgeon	Backus 1951
Percidae	*Percina caprodes**	Log Perch	Grant et al. 2001

port the hypothesis by Black et al. (1985) that populations would be discovered in the headwaters of the Churchill River drainage system. Water flows from Lake Shabogamo south into Shabogamo River, which flows into Ashuanipi River, and then through a series of rivers and lakes that eventually drain into the Smallwood Reservoir, which feeds the Churchill River.

Four Longnose Dace were captured on 27 June 2000 (53° 19.379′ N, 66° 26.608′ W) in the 1.25 cm mesh in 60 cm of water. The bottom substrate was composed of small boulders (25 cm - 100 cm in diameter) and cobble (6-24 cm). The water temperature was 10.6°C. Also caught at this site were 33 Lake Whitefish, 10 Lake Trout, 42 Longnose Sucker, 11 Round Whitefish and 27 Lake Chub. An additional single Longnose Dace was captured on 27 June 2000 (53° 19.540′ N, 66° 26.405′ W) in 2.54 cm mesh in 50 cm of water. The water temperature was 10.8°C. The bottom was flat and composed of small boulders (25 cm – 100 cm in diameter) and cobble (6-24cm). Other species caught at this site include 35 Lake Whitefish, 10 Lake Trout, 10 Longnose Sucker, 29 Round Whitefish, 186 Lake Chub and 2 Brook Trout.

The captured Longnose Dace body morphometrics were in the normal range for the species (Figure 2). They were black in colour with white undersides and dark lateral lines. The fish, on average, measured 75 mm in length and weighed 4.55 g. Fin structure was as follows: dorsal, 8 rays; left pectoral, 10 rays; pelvic, 7 rays; anal fin, 6 rays; and caudal fin, 18 rays. The fish scales were cycloid.

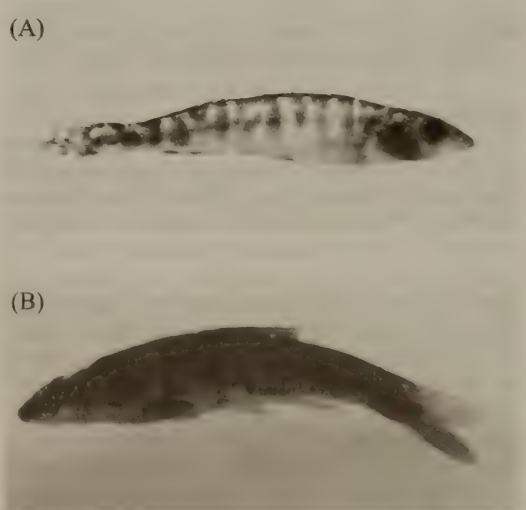


FIGURE 2. (A) Logperch, *Percina caprodes*, 77 mm long, weighing 3.5 g captured in Kapitagas Channel, western Labrador on 14 June 2000. (B) Longnose Dace, *Rhinichthys cataractae*, 75 mm long, weighing 4.55 g, captured in Lake Shabogamo, Labrador, on 27 June 2000.

Origin and Dispersal

Our discovery of the Logperch was approximately 150 km from the Grant et al. (2001) sampling area, suggesting that the species is well established in southern Labrador. This lends support to the hypothesis put forward by Black et al. (1985) that the Logperch is indigenous, arriving in the area through post-glacial dispersal.

Post-Wisconsin glacial dispersal for both the Logperch and the Longnose Dace into the Churchill River drainage basin was first hypothesized by Black et al. (1985), who indicated that species may have moved from the Great Lakes Basin to Glacial Lake Barlow-Ojibway, then north of the Otish Mountains of Quebec to the Churchill River headwaters, where they could invade Labrador to the north, east and south, and on into extreme east Quebec.

The suggestion by Power (1965) that the six Logperch he discovered in eastern Quebec were introduced to the Aguanus River by anglers as bait cannot be completely discounted, as both Lake Atikonak and Ashuanapi are near a transmission and railway line which runs between Sept-Îles in southeastern Quebec through southwestern Labrador, and north to Schefferville, Quebec. Conservation officers working in western Labrador report that it was common for trains to stop and give passengers an opportunity to fish in lakes that were adjacent to the railway line. In addition, hydro workers involved in the placement and construction of the transmission line may have inadvertently introduced the species when using live bait. However, this particular explanation is improbable because the Logperch cannot be held alive in pails for long periods (Scott and Crossman 1973). The Aguanus River is about 300 km east of the railway line (Figure 1).

Acknowledgments

Our thanks to Ken Curnew for ensuring the funding for the Labrador sampling program and to Conservation Officers Gary O'Brien, Mark Pritchett and Chuck Porter for their field assistance during the spring sampling program. A special thanks to Conservation Officer Lindo Watkins for both his field assistance and his suggestion to sample the Kapitagas Channel. Finally, a thanks to Roy Ficken of Memorial University of Newfoundland for taking the photos.

Literature Cited

Anderson, T. C. 1985. The rivers of Labrador. Canadian Special Publication in Fisheries and Aquatic Sciences. 81. 389 pages.

Backus, R. H. 1951. New and rare records of fishes from Labrador. Copeia 1951: 288–294.

Backus, R. H. 1957. The Fishes of Labrador. Bulletin of the American Museum of Natural History 113: 277–337.

Black, G. A., J. B. Dempson, and **W. J. Bruce.** 1986. Distribution and postglacial dispersal of freshwater fishes of Labrador. Canadian Journal of Zoology 64: 21–31.

Bruce, W. J., K. D. Spencer, and **E. Arsenault.** 1979. Mercury content data for Labrador fishes, 1977-78. Marine Services Data Report Number 142. iv + 263 pages.

Dempson, J. B. 1980. Present status of Pink Salmon (*Oncorhynchus gorbuscha)* in the Newfoundland Region. International Council for the Exploration of the Sea C.M. 1980/M:27.

Grant, S. M., E. E. Lee, J. R. Christian, and **R. A. Buchanan.** 2001. Occurrence of Logperch, *Percina caprodes*, in tributaries of Atikonak Lake, Labrador: a northeast range extension in Canada. Canadian Field-Naturalist 114: 685–668.

Hare, G. M. and **H. P. Murphy.** 1974. First record of the American shad (*Alosa sapidissima*) from Labrador waters. Journal of the Fisheries Research Board of Canada 19: 113–126.

Lear, W. H. 1975. Evaluation of the transplant of Pacific Pink Salmon (*Oncorhynchus gorbuscha)* from British Columbia to Newfoundland. Journal of the Fisheries Research Board (Canada) 32: 2343–2356.

Lester, N. P., M. M. Petzold, W. I. Dunlop, B. P. Monroe, S. D. Orasatti, T. Schaner, and **D. R. Wood.** 1991. Sampling Ontario Lake trout stocks: issues and standards: lake trout synthesis. Ontario Ministry of Natural Resources. Toronto. 117 pages.

Low, A. P. 1896. Report on the explorations in the Labrador Peninsula along the East Main, Koksaok, Hamilton Minicuagon and portions of other rivers in 1892-93-94-95. Annual Report of the Geological Survey of Canada New Series, Volume 8. For 1875, Appendix III. Queen's Printer, Ottawa, Ontario. 387 pages.

Murphy, H. P. 1972. A report of biological operations, Sand Hill River, Labrador, 1969, 1970 and 1971. Research and Development Branch, St. John's, Newfoundland. Progressive Report 89. 245 pages.

Power, G. 1965. Notes on the cold-blooded vertebrates of the Nabisipi River region county Duplessis, Quebec. Canadian Field-Naturalist 79: 49-64.

Ryan, P. M. 1980. Fishes of the Lower Churchill River, Labrador. Canadian Fisheries Marine Services Technical Report Number 922.

Scott, W. B., and **E. J. Crossman.** 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184. 966 pages.

Scott, W. B., and **M. G. Scott.** 1988. Atlantic Fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences 219. 731 pages.

Stearns. W. A. 1883. Notes on the natural history of Labrador. Proceedings of the United States National Museum 6: 111–137.

Weed, A. C. 1934. Notes on the sea trouts of Labrador. Copeia 1934: 127–133.

Received 2 January 2001
Accepted 25 February 2003

Notes on the *Populus* "Dripzone Effect" on Lichens in Well-ventilated Stands in East-central British Columbia.

TREVOR GOWARD[1,3] and ANDRÉ ARSENAULT

[1]Herbarium, Department of Botany, University of British Columbia, Vancouver, British Columbia V6G 2B11 Canada
[2]Southern Interior Forest Region, British Columbia Forest Service, 515 Columbia Street, Kamloops, British Columbia V2C 2T7 Canada
[3]Mailing address: Edgewood Blue, Box 131, Clearwater, British Columbia V0E 1N0 Canada

Goward, Trevor, and André Arsenault. 2003. Notes on the *Populus* "dripzone effect" on lichens in well-ventilated stands in east-central British Columbia. Canadian Field-Naturalist 117(1): 61–65.

The "dripzone effect" involves the above-ground transfer of nutrients — presumably in the form of leachates — from the upper crown of one tree species to the lower crown of another. In humid, poorly ventilated *Picea* stands, nutrient enrichment associated with *Populus* dripzones has been shown to promote the development of cyanolichens belonging to the *Lobarion*. Here we examine the same phenomenon in well-ventilated stands, in which members of the more xerophytic *Xanthorion* are favoured, while some species of the alectorioid lichen genus *Bryoria* are excluded. The latter phenomenon may partly account for the often discontinuous occurrence of *Bryoria* in many mixed conifer stands at lower elevations.

Key Words: Hair lichens, dripzone, *Populus, Xanthorion*, Wells Gray Park, British Columbia.

The microscale organization of epiphytic lichens in space and time reflects, in addition to chance, a complex interplay of environmental factors. Among the most important of these are diaspore availability, insolation, ventilation, humidity relations, chemical and textural properties of tree bark and wood, and nutrient input from extraneous sources (see James et al. 1977). Regarding the last factor, enrichment, several forms of extraneous nutrient input have been identified, including animal waste, atmospheric dust, long-range transport of industrial emissions in rain and snow, and precipitates from ocean spray, waterfalls, and fog (see Barkman 1958).

One enrichment phenomenon that has received little attention to date is the "dripzone effect"; i.e., the above-ground transfer of leachates from the upper canopy of one tree or shrub species to the lower canopy of another tree or shrub species growing nearby. Recently Goward and Arsenault (2000) documented a striking instance of the dripzone effect in the humid low-elevation forests of south-central British Columbia. Here the occurrence of neutrophytic cyanolichens (e.g., *Lobaria pulmonaria, Pseudocyphellaria anomala, Sticta fuliginosa*) was shown to be highest on *Picea* branches subject to calcium from the upper canopies of nearby *Populus* trees.

Our earlier study was conducted entirely in humid and poorly ventilated stands. A *Populus* dripzone effect, however, can also be discerned in stands that are both drier and well-ventilated. The primary objectives of this paper are to examine the impact of the dripzone effect on epiphytic lichen community structure in such stands, and to compare the resulting patterns with the earlier results of Goward and Arsenault (2000). Potential ecological implications inherent in our findings will also be briefly discussed.

Study Area

Our study was confined to *Picea* trees growing along the north bank of the Murtle River in Wells Gray Provincial Park, south-central British Columbia (51°58′N, 120°07′W). In its lower reaches, at about 800 m elevation, the Murtle River traverses the "Murtle Plateau", a flat-lying basaltic lava flow dating from the early Pleistocene overlaid by a mantle of weakly acidic glacial till and fluvioglacial deposits (Goward and Hickson 1996). The Murtle Plateau is located in a relatively humid region in which summer precipitation (May through September) averages roughly 260 mm (Environment Canada 1975a). Mean monthly temperatures range from -10°C in January to 15°C in July (Environment Canada 1975b). Air quality in this region is high (Anonymous 1990).

Vegetationally, our study area is representative of the moist-warm subzone of the Interior Cedar-Hemlock Zone (ICHmw: Lloyd et al. 1990), as well as the humid province of the Lower Oroboreal Subzone (Tuhkanen 1984; Goward and Ahti 1992). The tree layer consists primarily of *Abies lasiocarpa, Betula papyrifera, Picea engelmannii* × *glauca, Pinus contorta, Populus trichocarpa, P. tremuloides, Pseudotsuga menziesii*, and *Thuja plicata*. The forest cover is unmodified by human activity, and dates from an intense wildfire that swept southern Wells Gray Park in 1926 (Edwards 1954). For a more complete description, see Hämet-Ahti (1965) and Goward and Hickson (1996).

Material and Methods

Sampling

Field work was carried out in September and October 1999, and was restricted to the branches of *Picea engelmannii* × *glauca* aged 50 to 70 years

growing along a 1.5 km stretch of river judged to be relatively homogeneous for aspect, insolation, ventilation, humidity, and fire history. A major advantage of the study site is that *Populus* is restricted here to the immediate river margin, where the likelihood of nutrient "contamination" from *Populus* trees growing nearby is negligible.

Only ten trees could be found that met all of the above criteria. Of these, five were located within the dripzone of *Populus trichocarpa*; the others occurred at a distance of at least 15 to 20 m from the nearest *P. trichocarpa* canopy. Sampling was further restricted to *Picea* branches exposed to at least moderate ventilation. Only branches within 2 m of the ground were examined.

For each tree, we recorded diameter at breast height (dbh) and determined age using an increment borer. We also documented lichen frequency and abundance using a five-point scale (see Goward and Arsenault 1997), as follows: *1* = 2 or fewer colonies per tree; *2* = 3-5 colonies per tree; *3* = 6 colonies per tree, or up to 20% branch cover (under optimum conditions); *4* = 21% to 50% branch cover (under optimum conditions); and *5* = 51% branch cover or more (under optimum conditions). For ease of sampling, only those lichen species readily identified in the field were assessed; other species were collected and subsequently examined in the laboratory, but are not discussed here. Lichen taxonomy and nomenclature follow Esslinger and Egan (1995).

From each of the ten *Picea* trees examined, we collected dead corticate branches for assessment of bark pH. Sampling was restricted to the exposed, distal portions of branches on which a diverse assemblage of macrolichens was present. Branch segments supporting leprose lichens were assumed to signal microsites sheltered from precipitation (Tnsberg 1992), and therefore sheltered from canopy leachates; such branches were avoided.

All branch segments were later carefully stripped of bark and the bark was then air-dried, ground using a mechanical mill, and placed overnight in de-ionized water. pH readings were taken using a Fisher pH meter calibrated using buffers at pH 4.0 and pH 7.0. For a more detailed description of our methods, see Goward and Arsenault (2000).

Analysis

Epiphytic lichen community structure was examined using PCA and Spearman rank correlations between factor scores and the original vegetation matrix (for further details, see Goward and Arsenault 2000). Lichen frequency and abundance data are presented in Table 1, in which the species are

TABLE 1. Frequency and abundance of epiphytic macrolichens associated with *Picea* branches growing within (N = 5) and outside (N = 5) the *Populus* dripzone. Also shown are bark pH and Spearman rank correlation between frequency and abundance data and the scores of the first PCA axis. * = P<0.05, ** = P<0.01.

	Sampled trees										
	Within *Populus* Dripzone					Outside *Populus* Dripzone					
Lichen species	1	2	3	4	5	6	7	8	9	10	
Parmelia sulcata		1	2	3	1	1	3	2	2	3	0.14
Parmeliopsis hyperopta										1	0.17
Hypogymnia occidentalis								2			0.29
Hypogymnia austerodes	1	1	1			1		1	1	1	0.34
Alectoria sarmentosa		1			1	3	1		1	1	0.38
Bryoria fuscescens			1			1	3	3	1		0.44
Hypogymnia physodes		1	1	1		1		3	2	3	0.50
Hypogymnia imshaugii									1		0.52
Parmeliopsis ambigua						1		1			0.52
Tuckermannopsis chlorophylla						1	2		1	1	0.64*
Ramalina thrausta	1			2	1	3	3	1	2	3	0.66*
Platismatia glauca								1	2	1	0.67*
Bryoria capillaris	1			1		3	3	3	4	1	0.92**
Hypogymnia tubulosa		1	1	1		1	1	1			-0.14
Usnea lapponica	1	2	1	1			1	1	1		-0.21
Nephroma resupinatum					1						-0.41
Parmelia hygrophila					1						-0.41
Leptogium saturminum			1								-0.52
Physcia aipolia			2	1							-0.54
Lobaria pulmonaria			1		1						-0.70*
Melanelia subaurifera	3	3	3	3	2		1	1	1	1	-0.81**
Caloplaca holocarpa		1	1	1	1						-0.85**
Bark pH	4.54	5.3	5.76	5.22	5.5	4.84	4.69	4.73	4.67	4.98	0.79**

arranged across a similarity gradient to assist in interpretation. Differences in the frequency and abundance of species were further assessed using a Kruskall Wallis test. In addition, we included species occurring on *Picea* branches in the low ventilation sites discussed earlier by Goward and Arsenault (2000) for comparison.

The mean and standard deviations of bark pH were calculated for five branch samples occurring within the *Populus* dripzone and for five samples occurring outside the dripzone. Differences were assessed using a t-test.

Results and Discussion

Phorophytes

The *Picea* trees sampled varied from 50 to 70 years old, with an average age of 62 years. Their trunk diameters at breast height varied from 20 cm to 63 cm, with a mean of 36 cm. When trees occurring within and outside the *Populus* dripzone were compared, no significant difference could be noted for either tree age or diameter.

Bark pH

In an earlier study of 80 branch samples, *Picea* branches growing within the dripzone of *Populus* had a mean pH of 5.8, whereas similar branches growing at distance from *Populus* had a pH of 4.9 (Goward and Arsenault 2000). pH readings followed a similar trend in the present study. With the exception of a single outlier (see Table 1), bark pH was consistently higher within the *Populus* dripzone (mean pH = 5.2, 5.4 when outlier is excluded) than outside the dripzone (mean pH = 4.8). The outlier had a pH of 4.5, and possibly signaled a recent lowering of enrichment levels not yet reflected in the lichen flora. Bark is a dynamic substrate influenced by multiple factors; a certain amount of variation in bark pH is to be expected over time. When the outlier is excluded, the difference in bark pH between the two sets of branches changes from merely significant ($P < 0.05$) to highly significant ($P < 0.001$).

Epiphytic Lichen Community Structure

Principal Components Analysis performed on epiphyte abundance data separated the sampled trees into two distinct clusters along the first axis. These clusters correlate both with bark pH and with distance class from *Populus* (Figure 1). The first cluster is negatively correlated with the first axis, and incorporates lichens more or less restricted, on *Picea*, to the *Populus* dripzone. Predominating here are members of the *Xanthorion* alliance (i.e., *Caloplaca holocarpa, Physcia aipolia,* and *Melanelia subaurifera*) and, to a lesser extent, the *Lobarion* (i.e., *Leptogium saturninum, Lobaria pulmonaria,* and *Nephroma resupinatum*). Both the *Xanthorion* and the *Lobarion* are epiphytic alliances strongly associated with nutrient-rich substrates, though they differ in their moisture requirements (James et al. 1977).

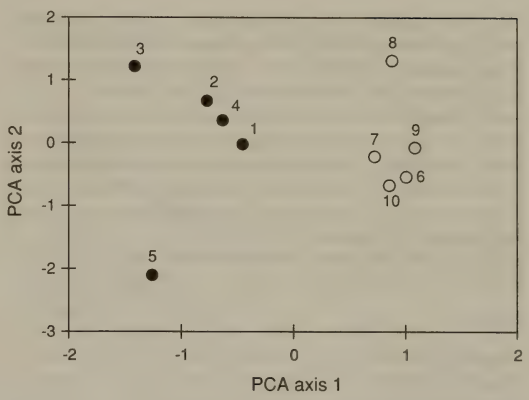


Figure 1. PCA ordination of epiphytic lichens occurring on branches of 10 *Picea* trees in Wells Gray Park. Numbers correspond with the tree numbers given in Table 1. Filled circles indicate trees occurring within *Populus* dripzone. Open circles indicate trees occurring outside the *Populus* dripzone.

The second species cluster is positively correlated with the first axis (Figure 1), and is associated predominantly with *Picea* branches growing outside the *Populus* dripzone. Those species denoted by an asterisk show significant correlation: *Alectoria sarmentosa, Bryoria capillaris*, B. fuscescens, Hypogymnia physodes, Parmeliopsis ambigua, Platismatia glauca*, Ramalina thrausta**, and *Tuckermannopsis chlorophylla**. All these species can be assigned to the *Pseudevernion* — an epiphytic alliance characteristic of acidic substrates (James et al. 1977). The general trend exhibited by the acidophytes accords well with the earlier findings of Goward and Arsenault (2000) (see also Table 2). One prominent exception is *Ramalina thrausta*, which would be classified as strongly acidophytic in this study, versus weakly neutrophytic in the earlier study. This species, however, appears to be rather ventilation-dependent (Wirth 1995); its distribution in the poorly ventilated stands of Goward and Arsenault (2000) probably reflects random litterfall events from conifer branches higher in the canopy.

During the course of field work, we repeatedly observed strong spatial variation in lichen community structure along the axis of most *Picea* branches. Neutrophytic lichens, if present at all, were generally restricted to the distal portions of the branches, whereas *Bryoria* and other acidophytic species occurred on the proximal portions of the same branches. We infer from this that nutrient enrichment increases in the direction of the branch tips, an observation in agreement with the "centrifugal" architecture of *Picea* (and most other conifers), in which canopy leachates should tend to be shed outwards from the trunk. In practice, however, probably only those branch segments exposed to weather are significantly enriched.

TABLE 2. Epiphytic lichens occurring on *Picea* branches, and significantly affected by the *Populus* dripzone effect in stands subject to high and low ventilation (present study and Goward and Arsenault 2000, respectively). "0" = species not present in study area; ns = no significant difference in abundance between species found within and outside the dripzone; + = abundance positively affected by the *Populus* dripzone; - = abundance negatively affected by the *Populus* dripzone; * = P<0.05, ** = P<0.01, as determined by Kruskall Wallis tests.

	Ventilation	
Species	Low	High
Bryoria capillaris	ns	-**
Bryoria fuscescens	ns	-*
Caloplaca holocarpa	0	+*
Hypogymnia austerodes	+*	ns
Hypogymnia occidentalis	-**	ns
Leptogium saturninum	+**	ns
Lobaria hallii	+*	0
Lobaria pulmonaria	+**	ns
Melanelia subaurifera	ns	+**
Nephroma resupinatum	+**	ns
Parmeliopsis ambigua	-**	ns
Parmeliopsis hyperopta	-**	ns
Platismatia glauca	-**	-**
Ramalina thrausta	ns	-*
Tuckermannopsis chlorophylla	ns	-*
Tuckermannopsis ciliaris	-**	0
Vulpicida pinastri	-*	0

The *Lobarion* versus the *Xanthorion*

When the results of this study are compared with data from the earlier study of Goward and Arsenault (2000), *Platismatia glauca* emerges as the only species shared by both studies that exhibits a significant (in this case negative) correlation with the *Populus* dripzone (Table 2). Nevertheless, a broad consistency in species response does exist. For example, members of the *Lobarion* (i.e., *Leptogium, Lobaria,* and *Nephroma*) associate with the dripzone in both studies, though they are much more frequent in the humid, poorly ventilated stands of the earlier study; presumably the drier, more ventilated conditions captured in the present study are somewhat inimical to them. Members of the *Xanthorion* (i.e., *Caloplaca, Melanelia,* and *Physcia*) are also favoured by the *Populus* dripzone in more xeric stands. Here it can be noted that the *Xanthorion* alliance is associated with rather dry habitats, being optimally developed, for example, in Mediterranean regions of Europe (James et al. 1977). The *Lobarion* alliance, by contrast, is restricted to moist localities, and is characteristic of rather oceanic or at least montane regions (Rose 1988; Goward and Arsenault, in preparation). Given the very different moisture requirements of these two alliances, the results reported were expected.

Alectorioid lichens

Goward (1998) has recently suggested that the microsite occurrence of *Bryoria* in high-elevation forests is controlled largely by sensitivity to prolonged wetting. Consistent with this hypothesis, *Bryoria* is poorly developed on sheltered conifer branches subject to heavy snow cover, but can be abundant on branches exposed to wind. Similar patterns are discernible also in low-elevation forests, though the microsite occurrence of *Bryoria* here is much less predictable on microclimatic grounds alone; presumably it is controlled by other environmental factors as well (Goward and Arsenault, in preparation). The present study points to a sensitivity to nutrient enrichment as an important ecological factor for at least some members of this genus.

As a rule, the bark of conifers is much more acidic than that of most hardwood trees (Barkman 1958). In this connection, it is probably not coincidental that alectorioid lichens show a strong preference for conifer bark (Brodo and Hawksworth 1977). The strong negative correlation between alectorioid abundance and nutrient-enriched *Picea* bark (Spearman rank correlation = -0.78) would seem to support this view — a conclusion further supported by the generally depauperate appearance of alectorioid thalli on nutrient-enriched *Picea* branches. *Bryoria*, for example, was repeatedly observed to be attached from the lower side of the supporting branch, having apparently lost through decay the initial point of contact on the opposing, upper side.

The negative correlation of *Alectoria sarmentosa, Bryoria capillaris,* and *B. fuscescens* with nutrient enrichment supports the earlier results of Goward and Arsenault (2000). In that study, however, both *A. sarmentosa* and *B. fuscescens* were significantly correlated with enrichment, whereas the only alectorioid species significantly correlated here is *B. capillaris*. Whether this reflects an actual physiological difference in the sensitivity of these species to enrichment, or whether it is an artifact of our present (rather meagre) data set is difficult to determine. In favour of the latter interpretation, both *A. sarmentosa* and *B. fuscescens* are much more abundant outside the *Populus* dripzone than within it (Table 1); nevertheless, they are simply too scarce in the present study to be included among the statistically significant species.

This study provides evidence in support of the hypothesis that the *Populus* dripzone effect can limit the small-scale occurrence of at least some alectorioid lichens. It remains to be determined whether the same phenomenon is capable of influencing alectorioid distribution at larger spatial scales as well. Here at least three questions should be explored: (1) does a *Populus* dripzone effect manifest itself on other tree species besides *Picea*; (2) might the presence of *Populus* act as a chemical barrier to alectorioid

dispersal from one conifer stand to another; and (3) could the *Populus* dripzone be partly responsible (in concert with the dripzones of other tree species!) for the patchy distribution characteristic of alectorioid lichens at lower elevations? The answers to these questions may be of some assistance in shaping future management policies pertaining to Flying Squirrels, Mountain Caribou, and other animal species dependent on a high biomass of alectorioid lichens.

Conclusions

When the results of this study are pooled with those of Goward and Arsenault (2000), at least three broad conclusions seem justified. First, depending on ambient moisture levels, the *Populus* dripzone effect promotes the colonization of *Picea* branches by members of either the *Lobarion* (humid conditions) or the *Xanthorion* (drier conditions). Second, at least some alectorioid lichens appear to be excluded by the dripzone effect. And third, the dripzone effect as a whole has potential to shed light on various critical, but often occult and therefore generally overlooked, chemical processes at work in mixed stands.

Acknowledgments

We thank Carla Rydholm for assistance in the laboratory. Jim Pojar, Carla Rydholm, and Kenneth G. Wright are thanked for constructive comments on the manuscript. John Karakatsoulis, of the University College of the Cariboo, Kamloops, kindly provided laboratory facilities and access to a pH meter. Funding for this project was provided by Forest Renewal B.C. and the British Columbia Ministry of Forests.

Literature Cited

Anonymous. 1990. Summary Information Package on Acid Rain Effects on Forests and Lakes of British Columbia. British Columbia Ministry of Environment Working Paper, Victoria.

Barkman, J. J. 1958. Phytosociology and ecology of cryptogamic epiphytes. van Gorcum, Assen.

Brodo, I. M., and **D. L. Hawksworth.** 1977. *Alectoria* and allied genera in North America. Opera Botanica 42: 1–164.

Edwards, R. Y. 1954. Fire and the decline of a mountain caribou herd. Journal of Wildlife Management 18: 521–526.

Environment Canada. 1975a. Canadian Normals. Volume 2-S1 (Precipitation). Downsview, Ontario.

Environment Canada. 1975b. Canadian Normals. Volume 1-S1 (Temperature). Downsview, Ontario.

Esslinger, T. L., and **R. S. Egan.** 1995. A sixth checklist of the lichen-forming, lichenicolous, and allied fungi of the continental United States and Canada. The Bryologist 98: 467-549.

Goward, T. 1998. Observations on the ecology of the lichen genus *Bryoria* in high elevation conifer forests. Canadian Field-Naturalist 112: 496–501.

Goward, T., and **T. Ahti.** 1992. Macrolichens and their zonal distribution in Wells Gray Provincial Park and its vicinity, British Columbia, Canada. Acta Botanica Fennica 147: 1–60.

Goward, T., and **A. Arsenault.** 1997. Notes on the assessment of lichen diversity in oldgrowth Engelmann Spruce - Subalpine Fir forests. Pages 67-78 *in* Sicamous Creek Silvicultural Systems Project: Workshop Proceedings. *Edited by* C. Hollstedt and A. Vyse. British Columbia Ministry of Forests, Victoria, British Columbia (Working Paper 24/1997).

Goward, T., and **A. Arsenault.** 2000. Cyanolichen distribution in young unmanaged forests: a dripzone effect? Bryologist 103: 28-37.

Goward, T., and **C. Hickson.** 1996. Nature Wells Gray. A Visitors' Guide to the Park. Lone Pine Publishing, Edmonton, Alberta.

Hämet-Ahti, L. 1965. Notes on the vegetation zones of western Canada, with special reference to the forests of Wells Gray Park, British Columbia. Annales Botanici Fennici 2: 274–300.

James, P. W., D. L. Hawksworth, and **F. Rose.** 1977. Lichen communities in the British Isles: a preliminary conspectus. Pages 295–413 in. Lichen Ecology. *Edited by* M. R. D. Seaward. Academic Press, London.

Lloyd, D., K. Angove, G. Hope, and **C. Thompson.** 1990. A guide for site identification and interpretation of the Kamloops Forest Region. Volumes 1 and 2. British Columbia Ministry of Forests, Land Management Handbook 23: 1–399.

Rose, F. 1988. Phytogeographical and ecological aspects of *Lobarion* communities in Europe. Botanical Journal of the Linnean Society 96: 69–79.

Tnsberg, T. 1992. The sorediate and isidiate, corticolous, crustose lichens in Norway. Sommerfeltia 14: 1–331.

Tuhkanen, S. 1984. A circumboreal system of climatic-phytogeographical regions. Acta Botanica Fennica 127: 1–50.

Wirth, V. 1995. Die Flechten Badden-Württembergs. Teil 2. Eugen Ulmer, Stuttgart.

Received 22 January 2001
Accepted 30 April 2003

Eco-geographical and Cytological Notes on the Entire-leaved Daisy, *Hulteniella integrifolia* (Asteraceae), in Québec

NORMAN DIGNARD[1] and CAMILLE GERVAIS[2]

[1]Ministère des Ressources naturelles, de la Faune et des Parcs, Herbier du Québec, 2700 rue Einstein, Sainte-Foy, Québec G1P 3W8 Canada

[2]Herbier Louis-Marie, Pavillon Charles-Eugène-Marchand, Université Laval, Sainte-Foy, Québec G1K 7P4 Canada (Deceased 28 November 2002)

Dignard, Norman, and Camille Gervais. 2003 Eco-geographical and cytological notes on the Entire-leaved Daisy, *Hulteniella integrifolia* (Asteraceae), in Québec. Canadian Field-Naturalist 117(1): 66–69.

Hulteniella integrifolia is reported from the Puvirnituq and Déception rivers in Nunavik (Nouveau-Québec). Its habitat (along the Puvirnituq River) is described and its companion species are listed. The morphology and the number of chromosomes (2n=18) are identical to previously reported specimens elsewhere in its range. *H. integrifolia* was recently added to the list of the endangered or vulnerable plant species in Québec.

Key Words : *Hulteniella integrifolia, Chrysanthemum integrifolium,* Asteraceae, Entire-leaved Daisy, Nunavik, Nouveau-Québec flora, rare plants, range extension.

While conducting floristic field work in the Nouveau-Québec Crater region in August 1998, the first author discovered two small populations of the Entire-leaved Daisy, *Hulteniella integrifolia* (Richards.) Tzvel. [synonyms : *Arctanthemum integrifolium* (Richards.) Tzvel.; *Chrysanthemum integrifolium* Richards.; *Dendranthema integrifolium* (Richards.) Tzvel.; *Leucanthemum integrifolium* (Richards.) DC.], along the Puvirnituq River, 20 km northwest of the crater. Earlier reports of the species in Québec from Marie-Victorin (1935, 1964, 1997), Scoggan (1978-1979), Porsild and Cody (1980) (map shows a dot in the Quaqtaq area) and Cody (1996) were undocumented as searches in herbaria housing major collections from the eastern Canadian Arctic (BM, C, CAN, DAO, E, G, H, K, MT, MTMG, P, QFA and US) did not locate a justifying specimen. These reports are presumably based on collections from Akpatok island in the Ungava Bay or from the Coats and Nottingham islands in the Hudson Strait (Polunin 1940), which all rest within the Northwest Territories (now the Nunavut). Curiously, the plant did not appear in the two first lists of rare, vulnerable or threatened plants of Québec (Bouchard et al. 1983; Lavoie 1992). Our searches in the above mentioned herbaria have, however, led to the discovery of a specimen at the Botanical Museum of Helsinki (H) that was collected along the Déception River in 1986.

Eco-geography

Hulteniella integrifolia is a low-arctic and subarctic amphiberingian species. Its range extends from northern Québec and Ellesmere Island (north to Lake Hazen 81°50′N, 71°05′W) westward to Yukon, Alaska and eastern Siberia. Few isolated populations occur in northern British Columbia (Hultén 1968). In the eastern Arctic (Figure 1), *H. integrifolia* grows chiefly in areas of exposed calcareous tundra, gravel, solifluxion soil and rocky slopes, also occasionally on alluvial terraces flooded in early summer but otherwise dry. Vegetation is dominated by the shrubs *Dryas integrifolia*, *Cassiope tetragona*, *Salix arctica*, by the terricolous lichens *Cladina mitis*, *Flavocetraria nivalis* and *Alectoria ochroleuca* and to a much lesser extent by the bryophytes *Ptilidium ciliare*, *Polytrichum piliferum*, *Aulacomnium turgidum, Dicranum elongatum* and *Polytrichastrum alpinum*. Herbaceous species include sedges and forbs whose number and cover vary greatly with the exposure, the microrelief and the humidity. Commonest companion species are listed in Table 1.

In full bloom, this clump-forming beautiful little daisy is unmistakable with its pure white rays, its brownish scarious-margined bracts and its short basal linear leaves (Figure 2a). Stems may vary from 2 to 15 cm in height. The degree of pubescence on the stem seems to be age-related to a certain degree, being white-lanate when young and more or less villous when mature. It can be easily overlooked when growing among *Dryas* clones, especially when the rays are withered and the stems short.

Hulteniella integrifolia is ranked S1 in Québec (Labrecque and Lavoie 2002) and S2S3 in British Columbia (Douglas et al. 1998).

Cytological Observations

The chromosome number 2n=18 (Figure 2b) for this taxon in Québec, the easternmost part of its range, is identical to those previously published from each side of the Bering Strait (Zhukova 1965; Johnson and Packer 1968, etc.), from Central Alaska (Knaben 1968) and from British Columbia (Packer 1968), near the westernmost limit of the species range.

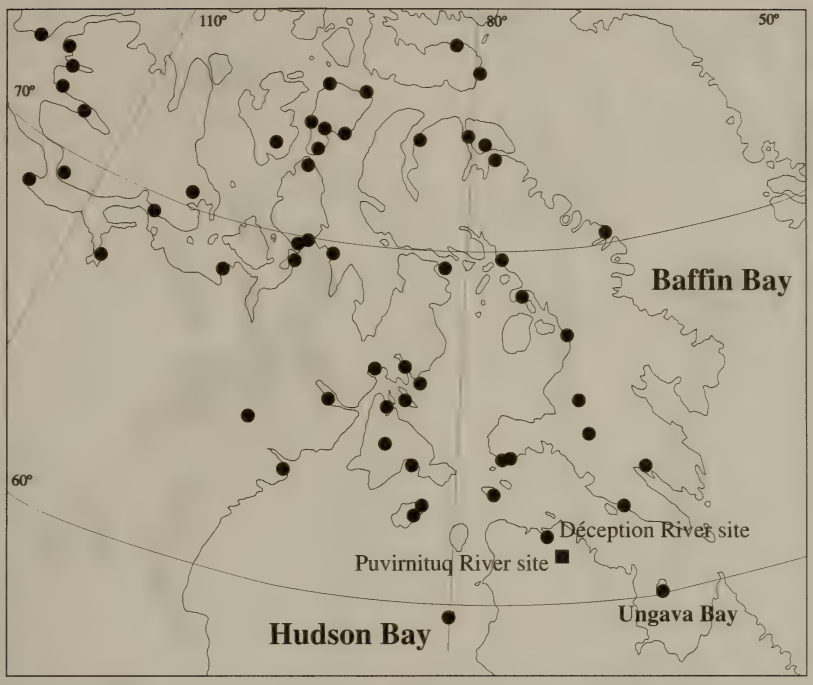


FIGURE 1. Distribution of *Hulteniella integrifolia* in Northern Québec and in the southeastern part of the Canadian Arctic Archipelago [CAN, DAO, MT, QFA, QUE, Polunin (1940) and Porsild and Cody (1980)]. The square indicates the population from which a chromosome count was obtained.

TABLE 1. Vascular species associated with *Hulteniella integrifolia* in northern Québec.

Species	Puvirnituq River	Akpatok Island[1]
Cassiope tetragona	×	×
Dryas integrifolia	×	×
Salix arctica	×	×
Salix herbacea	×	×
Salix reticulata	×	×
Carex misandra	×	×
Carex nardina	×	–
Carex scirpoidea	×	–
Cerastium alpinum	×	–
Chamerion latifolium	×	–
Hierochloe alpina	×	×
Oxytropis deflexa	×	–
Poa arctica	×	–
Persicaria vivipara	×	×
Saxifraga aizoides	×	×
Saxifraga oppositifolia	×	×
Silene acaulis	×	–
Tofieldia pusilla	×	×

[1]Polunin (1934)

One of the nine chromosome pairs from the studied individual is subtelocentric (Figure 2b, arrows) while the eight other pairs are metacentric or submetacentric. This pattern is also apparent in figure 42 of Knaben (1968) for an Alaskan individual. Though the Puvirnituq River population seems to be very isolated, it lacks evident chromosomal structural changes that are sometimes present in such disjunct populations (Verlaque et al. 1991).

Voucher material

QUÉBEC : Déception River. *Ca.* 30 miles north of Asbestos Hill, 3 km from the road on a riverside terrace, 62°07′30″N-74°17′00″W, alt. 50 m, *M. Seppälä s.n.*, August 14 1986 (H 1570910); Gorges de la rivière Puvirnituq à la hauteur du lac Carré, rive sud, 61°24′52″N-73°56′06″W, alt. 400 m, *N. Dignard 98-509*, 13 août 1998 (QUE 115624); *Idem*, rive nord, 61°24′54″N-73°55′33″W, alt. 380 m, *N. Dignard 98-584*, 15 août 1998 (QUE 115539); Rivière Puvirnituq, 1,3 km en amont de l'embouchure de la décharge du lac Perron, 61°25′03″N-73°53′25″W, alt. 420 m, *N. Dignard & J. Gagnon 00-226*, 7 août 2000 (QUE 116678).

Acknowledgments

The authors are grateful to the curators of the selected herbaria for their assistance, to the Société de la faune et des parcs du Québec for the logistics of the field work and to Dr. Matti Seppälä (University of Helsinki) for his data on the Déception River collection site.

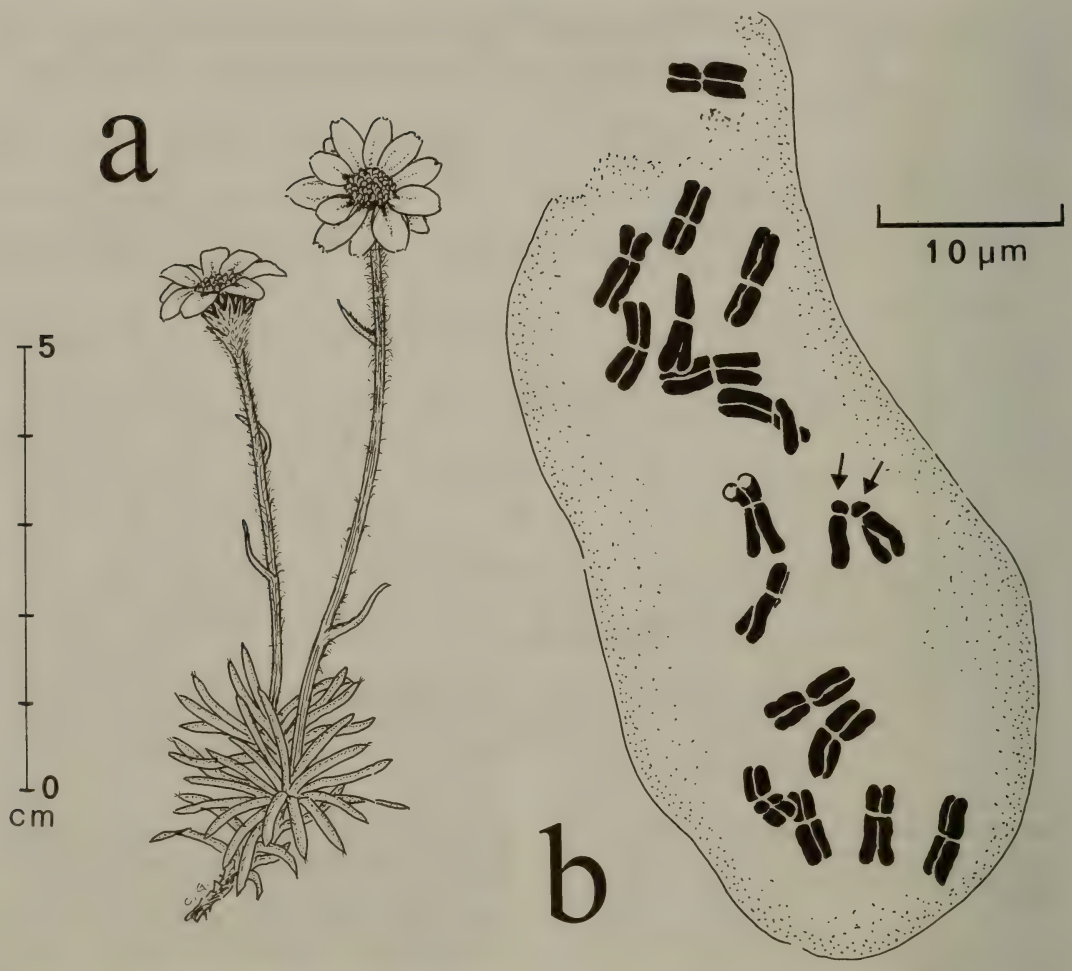


FIGURE 2. (a) *Hulteniella integrifolia* (Richards.) Tzvel., young flowering individual; (b) root tip chromosomes from a Puvirnituq River specimen (2n=18). Arrows indicate a pair of subtelocentric chromosomes (pretreatment: colchicine 0.3% for 2 1/2 hours).

Literature cited

Bouchard, A., D. Barabé, M. Dumais, et **S. Hay.** 1983. Les plantes vasculaires rares du Québec. Syllogeus (48). 79 pages.

Cody, W. J. 1996. Flora of the Yukon Territory. NRC Research Press, Ottawa. 643 pages.

Douglas, G. W., G. B. Straley, and **D. V. Meidinger.** 1998. Rare native vascular plants of British Columbia. B.C. Ministry of Environment, Lands & Parks. Victoria. 423 pages.

Hultén, E. 1968. Flora of Alaska and neighboring territories. Stanford University Press, Stanford. 1008 pages.

Johnson, A. W., and **J. G. Packer.** 1968. Chromosome numbers in the flora of Ogotoruk Creek, N.W. Alaska. Botaniska Notiser 121: 403–456.

Knaben, G. 1968. Chromosome numbers of flowering plants from Central Alaska. Nytt Magasin foer Botanikk (Oslo) 15: 240–254.

Labrecque J., et **G. Lavoie.** Les plantes vasculaires menacées ou vulnérables du Québec. Gouvernement du Québec, ministère de l'Environnement, Direction du patrimoine écologique et du développement durable, Québec. 200 pages.

Lavoie, G. 1992. Plantes vasculaires susceptibles d'être désignées menacées ou vulnérables au Québec. Gouvernement du Québec, ministère de l'Environnement, Direction de la conservation et du patrimoine écologique, Québec. 180 pages.

Marie-Victorin, Fr. 1935. Flore laurentienne. Imprimerie de la Salle, Montréal. 917 pages.

Marie-Victorin, Fr. 1964. Flore laurentienne. 2e édition revue et mise à jour par E. Rouleau. Les Presses de l'Université de Montréal, Montréal. 924 pages.

Marie-Victorin, Fr. 1997. Flore laurentienne. 3e édition mise à jour et annotée par L. Brouillet, S. G. Hay, I. Goulet, M. Blondeau, J. Cayouette et J. Labrecque. Les Presses de l'Université de Montréal, Montréal. 1093 pages.

Packer, J. G. 1968. *In* IOPB Chromosome number reports. Taxon 17: 285–288.

Polunin, N. 1934. The vegetation of Akpatok Island. Part I. Journal of Ecology 22: 337–395.

Polunin, N. 1940. Botany in the Canadian Eastern Arctic. Part I. Pteridophyta and Spermatophyta. National Museum of Canada, Bulletin (92), Ottawa. 408 pages.

Porsild, A. E., and **W. J. Cody.** 1980. Vascular plants of continental Northwest Territories. National Museum of Natural Sciences, Ottawa. 667 pages.

Scoggan, H. J. 1978-1979. The flora of Canada. National Museum of Natural Sciences, Publications in Botany 7 (1), Ottawa, 4 volumes. 1711 pages.

Verlaque, R., A. Aboucaya, M. A. Cardona, and **J. Contandriopoulos.** 1991. Quelques exemples de spéciation insulaire en Méditerranée occidentale. Botanika Chronika 10: 137–154.

Zhukova, P. G. 1965. Kariologicheskaya kharakteristika nekotorykh rasteniy Chukotskogo polyostrova. Botanicheskii Zhurnal 50: 1001–1004.

Received 26 January 2001
Accepted 4 July 2003

Status of the Largest Breeding Concentration of Atlantic Puffins, *Fratercula arctica,* in North America

MICHAEL S. RODWAY[1,3], HEIDI M. REGEHR[1,3], and JOHN W. CHARDINE[2]

[1]Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9 Canada
[2]Canadian Wildlife Service, P.O. Box 6227, Sackville, New Brunswick E4L 1G6 Canada
[3]Current address: Department of Biological Sciences, Simon Fraser University Burnaby, British Columbia V5A 1S6 Canada

Rodway, Michael S., Heidi M. Regehr, and John W. Chardine. 2003. Status of the largest breeding concentration of Atlantic Puffins, *Fratercula arctica*, in North America. Canadian Field-Naturalist 117(1): 70–75.

Suspected declines due to oil pollution, accidental entrapment in fishing gear, expanding gull populations, and the Capelin (*Mallotus villosus*) fishery have generated concern for the Atlantic Puffin (*Fratercula arctica*) population in the western Atlantic. The majority of that population breeds on three islands within the Witless Bay Seabird Ecological Reserve off the southeast coast of Newfoundland. We conducted a census of the numbers of puffins breeding on the largest colony there on Great Island in 1993-1994. The product of three component measurements, colony area of 15.2 ha, average burrow density of 0.92 ± 0.04 burrows/m^2, and average burrow occupancy rate of 87.9 ± 3.1%, gave a breeding population estimate of 123 000 ± 7 000 pairs. Most of the difference between our estimate and a previous estimate of 52 000 pairs from 1979 was attributed to the fact that burrow occupancy in 1979 was determined during the late chick stage after many eggs and chicks would have failed, thus giving a lower estimate of the number of pairs initiating breeding. Similar burrow density in 1979 and 1994, and expansion of colony area from 12.9 to 15.2 ha, mainly due to colonization of interior habitat, provided evidence that the breeding population of Atlantic Puffins on Great Island has expanded in recent years.

Key Words: Atlantic Puffin, *Fratercula arctica*, Great Island, census, populations, survey methods, Newfoundland.

Breeding colonies of Atlantic Puffins (*Fratercula arctica*) in the northwest Atlantic were severely reduced or eliminated by hunting, egg collecting, habitat destruction, and the introduction of domestic animals throughout the 18th and 19th centuries (Drury 1973-1974; Nettleship and Evans 1985). Most colonies were eliminated in the Gulf of Maine and Bay of Fundy, and numbers were greatly reduced in Newfoundland, Labrador, and along the north shore of the Gulf of St. Lawrence (Bent 1919). Reduction of human exploitation allowed puffin populations to recover partially during the early and mid-20th century. However, factors such as mortality from oil pollution, accidental entrapment in fishing nets, fisheries impacts on Capelin (*Mallotus villosus*)—the puffins' primary summer prey (Rodway and Montevecchi 1996)—and increasing numbers of kleptoparasitic and predatory Herring (*Larus argentatus*) and Great Black-backed (*L. marinus*) gulls, have renewed concern for Atlantic Puffin populations since the 1970s (Nettleship and Evans 1985; Nettleship 1996).

Since at least the mid-1960s, a significant proportion of the North American Atlantic Puffin population has bred on three islands (Gull, Green, and Great) within the Witless Bay Seabird Ecological Reserve off the southeast coast of Newfoundland (Nettleship and Evans 1985). Observations of puffins nesting in Witless Bay date from the mid-19th century, but quantitative estimates were not attempted until 1967 when D. N. Nettleship and L. M. Tuck made preliminary estimates of 75 000 pairs on Gull, 20 000 pairs on Green, and 100 000 pairs on Great islands (Nettleship and Evans 1985). More detailed surveys gave estimates of 60 000, 17 000, and 148 000 pairs in 1973 (Nettleship and Evans 1985), and 30 000, 9300, and 52 000 pairs in 1979 (Cairns et al. 1989) for Gull, Green, and Great islands, respectively.

Different methods used in 1973 and 1979 made comparisons difficult and prevented conclusions that breeding numbers had really declined during that period (Cairns and Verspoor 1980*; Nettleship, unpublished data). However, other evidence suggests that puffin numbers have declined in the past on Great Island. Small sections of the colony showed reductions of 22-25% in the number of burrows recorded between 1973 and 1979 (Cairns and Verspoor 1980*; Nettleship, unpublished data), and counts of adults in attendance early in the season at one study plot declined 76% between 1974 and 1981 (Nettleship et al. 1989*).

We estimated the numbers of Atlantic Puffins breeding on Great Island in 1993-1994, using methods that could be easily replicated for future comparisons. We also mapped the distribution of different vegetation types that may be related to the activities of nesting birds (Harris 1984). We confined our efforts to Great Island because it is the largest colony in the northwest Atlantic, most previous data indicating population declines pertained to that colony, and limited resources allowed a thorough survey of only

*See Documents Cited section

one major colony. We compare our results to previous studies, and extrapolate conclusions about the status of the Great Island breeding population to the Witless Bay population as a whole.

Methods

Great Island (47° 11′ N, 52° 46′ W) is part of the Witless Bay Seabird Ecological Reserve and lies approximately 2.4 km offshore of southeast insular Newfoundland (Figure 1). The island has been described in detail by Nettleship (1972).

Three component measurements were used in the calculation of a breeding population estimate for puffins on Great Island: burrow density, the proportion of burrows that were occupied by nesting birds (occupancy rate), and colony area (Nettleship 1976; Evans 1980; Bibby et al. 1992). Burrow occupancy was determined on 17-28 June 1993 as part of a larger study on puffins in 1992-1993 (Rodway et al. 1998). Burrow density was determined and colony area mapped 22 July to 8 August 1994 (more details are given in Rodway et al. 1996*).

Burrow density was estimated by calculating the average density of burrows in 237 sample quadrats. Quadrats were distributed using a stratified, centred start, systematic sampling scheme (Madow 1953) to ensure adequate representation of different parts of the colony. Ten permanently marked parallel transects, 100 m apart, were run east and west across the island from a centre line measured down the long axis of the island (Figure 2). Quadrats 2 × 2 metres in size were established at 5 m intervals throughout the puffin colony along each transect. Numbers of burrows were counted and angle of slope was measured to the nearest degree in each quadrat. An entrance was called a burrow if its tunnel extended more than 50 cm and did not connect with another entrance within 100 cm. In rare cases, tunnels less than 50 cm were called burrows if they contained obvious nest cups, eggs, or chicks.

Occupancy rate was determined by a single check of a sample of burrows during the mid-incubation period. This provided a conservative estimate of burrow occupancy because some eggs may have been lost before or laid after burrows were checked. Occupancy was determined in 140 burrows (28 plots of five burrows each). Sample plots were stratified by habitat and location to minimise possible biases due to position in the colony (see Nettleship 1972; Rodway et al. 1998). A burrow was considered

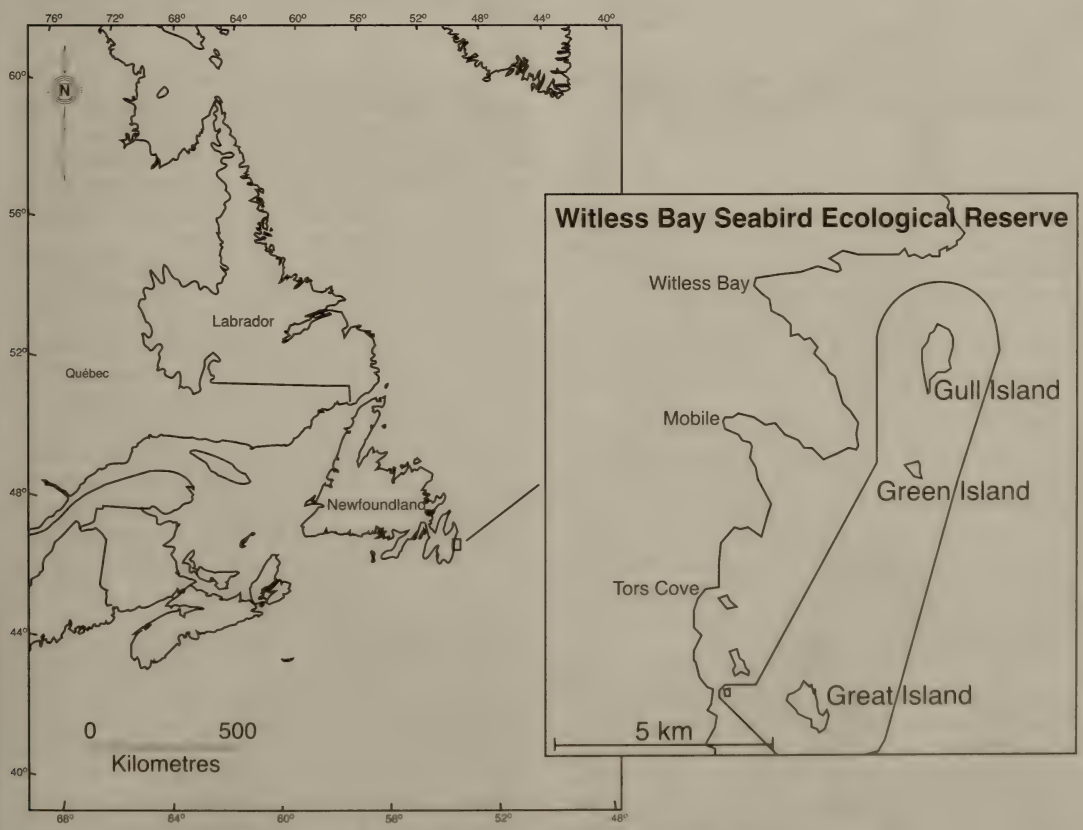


FIGURE 1. Location of Great Island and Witless Bay Seabird Ecological Reserve, Newfoundland.

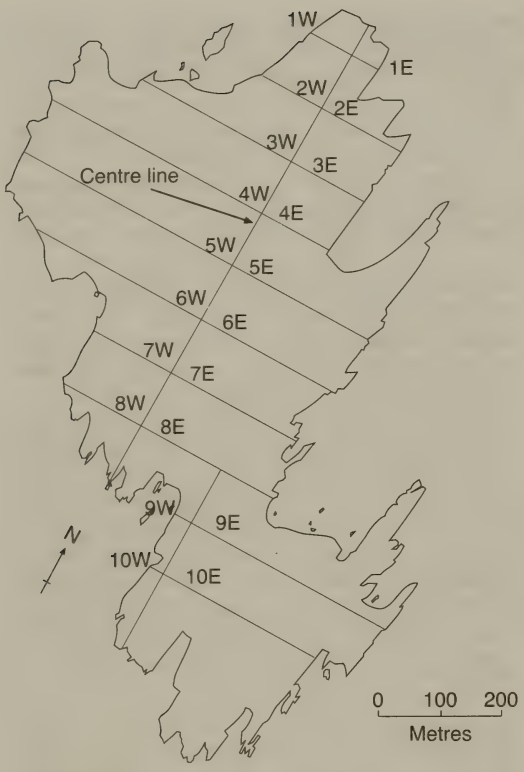


FIGURE 2. Location of permanently marked transects on Great Island, Newfoundland.

occupied if an egg was found. Burrows were considered empty if all tunnel branches were explored and no egg was found. Exploring burrows longer than an arm's reach required the careful digging of one or more conical access holes until the end was reached. Excavated holes were immediately patched with sticks and soil to ensure their future integrity. To minimize disturbance, adults and eggs were not removed from burrows.

All portions of the island where burrows occurred were included in the measurement of colony area. Colony boundaries and boundaries of vegetation types were measured to the nearest 0.1 m along transects. Colony and vegetation boundaries outside transects were determined by careful exploration and by measurements taken perpendicular to transect lines. Measurements were taken along the ground and thus include surface contours.

Distance and slope measurements taken along transects, as well as during exploration, were used to draw colony areas on a detailed topographic map at a scale of 1:943 with 10-foot contour intervals. The horizontal surface area of the colony was measured on the map with a Koizumi compensating polar planimeter, Type KP-23. Colony areas were divided into sections with similar slopes. Adjusting for slope, the area of individual sections was given by:

$$C_s = A_h T^2 (\cos Q)^{-1},$$

where C_s is the colony surface area, A_h is the area on the map, T is the scale of the map, and Q is the mean slope along the transects or, if measured areas did not fall along transects, the average slope calculated from the spacing of the 10′ contour lines. To improve accuracy, each small section delimited on the map was measured three times with the planimeter, and the mean of those three measures was used to calculate the area. Colony area calculations took into account the average uphill slope, but not the undulations between quadrats or between transects. Therefore our calculations give a conservative estimate of the total surface area available to birds for nesting.

The total number of burrows in the colony (B) is the product of the overall average density of burrows, as determined in the quadrats, and the total area of the colony. B multiplied by the occupancy rate (R) gives an estimate of total nesting pairs (P). The standard error (SE) of P is calculated as follows:

$$SE(P) = (B^2 \text{ Variance}(R) + R^2 \text{ Variance}(B) - \text{Variance}(B) \text{ Variance}(R))^{1/2}$$

(Rodway et al. 1996*. Means are quoted plus or minus one standard error.

Results

Vegetation above a precipitous, rocky shoreline changed from steep, grassy slopes to level or gently sloping, perimeter grassy areas, grass-*Rubus* meadows, and finally to a central Balsam Fir (*Abies balsamea*)/Black Spruce (*Picea mariana*) forest (Figure 3). Central, forested habitat was confined to the wider, northern part of the island.

Puffins nested in all grassy, perimeter areas with enough soil to support burrows and on inland slopes as far as 200 m from shore (Figure 4). Most burrows occurred in unforested grassy or bare peat areas. Along the northeast side of the island, especially in the vicinity of transect 3E, burrows extended as far as 17.5 m into forested habitat. New burrows were being dug under trees in that area and in tall meadow grasses interior to the main burrowed slopes along the north end of the island. Pockets of old tussocks along the west side, in Nettleship's "main colony" plot (see Nettleship 1972), and in the meadow on the outer, east side of the island appear to have been abandoned due to erosion.

Burrow density in all sampled quadrats averaged 0.92 ± 0.04 burrows/m^2 (N = 237). Sampled area was 0.6% of the colony area. Proportions of burrows with eggs during the mid-incubation period averaged 87.9 ± 3.1% (N = 28). Total area of puffin colony measured 151 936 m^2 or 15.2 ha.

Burrow density multiplied by the colony area gave an estimate of 140 070 ± 6245 burrows, which, at an

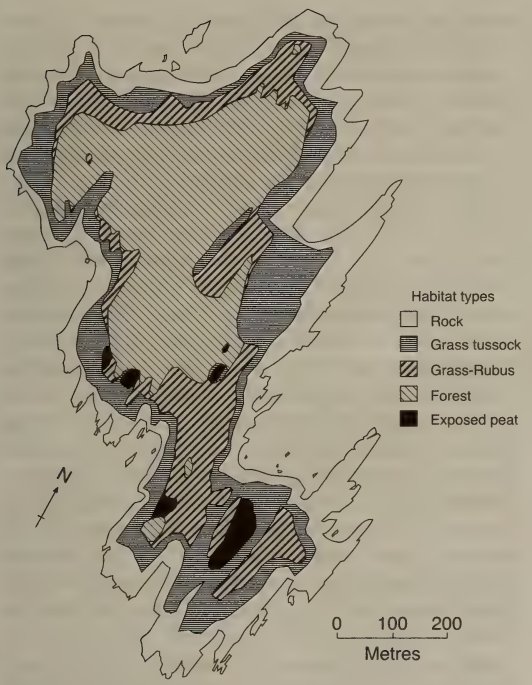


FIGURE 3. Distribution of vegetation types on Great Island, Newfoundland, in 1994.

occupancy rate of 0.88 ± 0.03 breeding pairs/burrow, yields a breeding population estimate of 123 066 ± 7029 pairs. Rounding off, we estimate the current breeding population of Atlantic Puffins on Great Island to be 116 000 – 130 000 pairs.

Discussion

Comparison of the present vegetation distribution (Figure 3) with that in 1968-1969 (Figure 2 in Nettleship 1972) indicated that forested area has contracted and perimeter grassy and meadow habitats have expanded. Long-term residents that have fished around Great Island throughout this century report similar observations (J. Reddick, personal communication). Changes are especially obvious on the southern end, which is now virtually devoid of forest, and along the eastern and northern sides of the island. The activities of nesting birds, particularly puffins and Herring Gulls (*Larus argentatus*), likely contributed to habitat changes.

Our estimate of 123 000 pairs of Atlantic Puffins nesting on Great Island in 1993-1994 probably underestimates the actual number nesting due to two sources of bias inherent in our methodology. First, the area of the colony was likely underestimated because of the complex, fractal nature of natural habitats (Pennycuick and Kline 1986). We corrected our colony area estimate to account for differing slopes in quadrats spaced 5 m apart along transects, which were spaced 100 m apart. However, smaller hills or valleys between quadrats or transects would not have been characterized at our scale of measurement. Second, occupancy rates may have been underestimated because any burrow in which an egg had been lost and not replaced before the single check during incubation would not be considered occupied. Although the present estimate is conservative, results from future surveys using the same methodology should be comparable.

Our 1993-1994 estimate was over double the latest previous estimate of 52 000 pairs obtained in 1979 (Cairns and Verspoor 1980*; Nettleship, unpublished data). The current estimate is closer to the earlier one of 148 000 pairs made in 1973 (Nettleship and Evans 1985). A detailed account of the methods used in the 1973 survey has not been published and so we were unable to compare our estimate with that one. Methods used in 1979 (Cairns and Verspoor 1980*) were in general similar to those used in this study, and some comparisons are possible.

The difference in the population estimates from 1979 (Cairns and Verspoor 1980*) and 1993-1994 was due to a lower occupancy rate in 1979 (44.1 vs.

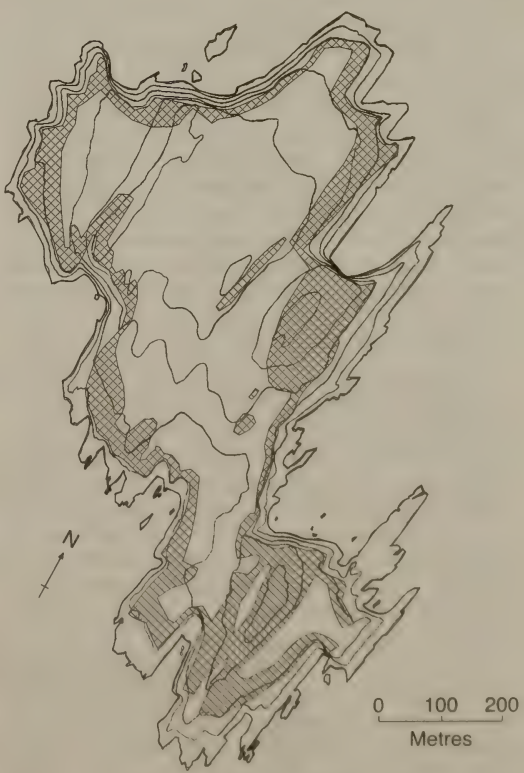


FIGURE 4. Atlantic Puffin colony (shaded) on Great Island, Newfoundland, in 1994. Contour lines are at 50-foot intervals.

87.9%), and larger colony area estimate in 1994 (15.2 vs. 12.9 ha). Differences in occupancy rates and area estimates accounted for 86% and 14%, respectively, of the difference in population estimates between the two years. Burrow densities in 1994 and 1979 were very similar (0.92 ± 0.04 vs. 0.91 ± 0.4 burrows/m^2, respectively).

The occupancy rate in 1979 was much lower than in 1993 because in 1979 burrow occupancy was determined during the late chick stage. In so doing, burrows in which an egg or chick was lost without replacement before the census were not considered occupied and, as a result, observed occupancy rates in 1979 were lower. Also, proportions of adult puffins that initiate breeding vary in response to environmental conditions, resulting in potentially large inter-annual changes in burrow occupancy rates (Ashcroft 1979; Harris and Murray 1981). Because occupancy rates depend to a large degree on breeding success up to the time of the survey, lower breeding success could also contribute to lower occupancy rates recorded in 1979. Breeding success indeed was lower on nearby Gull Island (Figure 1) in 1979 (Rice 1985) than on Great Island in 1993 (Rodway et al. 1998). Therefore, we conclude that the lower occupancy rate estimated in 1979 was likely due to lower breeding success and the later date when occupancy was determined.

Over most of Great Island, the distribution of puffin nesting habitat was similar in 1979 (Cairns and Verspoor 1980*) and 1994; however, expansion has taken place in some areas over the intervening period. Greatest differences between colony areas mapped in the two years are the existence of pockets of nesting habitat along transect 7E in 1994 that were absent in 1979, and more extensive nesting on inland slopes along transect 5E and on level habitat along the western and northern sides of the island in 1994. New burrows being dug under forest and in tall meadow grasses interior to main burrowed areas in 1994 also suggested that the Great Island colony is expanding inland. Contraction has also taken place as birds have abandoned some older, eroded areas. Abandoned areas were not included in calculations of colony area, and the larger area estimate in 1994 suggests that expansion has outweighed contraction over the intervening years. Thus, there seems to be sufficient evidence to accept the larger colony area estimate in 1994 as indicative of real colony expansion since 1979, if we assume that exploration of the island was equally thorough and that mapping was equally accurate in the two surveys. Both assumptions are likely. Permanently marked transects and measured distances to colony boundaries along those transects in 1994 will allow more definitive conclusions about future changes in the extent of puffin nesting habitat on Great Island.

Given that burrow density was similar in 1979 and 1994, the increase in colony area suggests that the breeding population of Atlantic Puffins on Great Island has expanded in recent years. Reported increases of over 50% in breeding populations at colonies along the North Shore of the Gulf of St. Lawrence over a similar time period (Chapdelaine 1995) suggest that upward trends may be more widespread in the Northwest Atlantic.

Our results contrast with previously reported declines of 25-35% in puffin populations on Great Island from 1972 to 1989 (Nettleship and Evans 1985; Nettleship 1996). Previous estimates of population change were based on counts of burrows in small sections of the colony in 1973 and 1979 (Nettleship and Cairns, unpublished data) and on multiple counts of puffins attending one study site early in the season (Nettleship et al. 1989*). Anker-Nilssen and Røstad (1993) found that monitoring numbers of burrows in few, selected plots within a colony provided biased estimates of whole-colony changes. Differences found among habitats and locations on Great Island (Nettleship 1972; Rodway et al. 1998) emphasize the importance of unbiased sampling throughout the colony to determine burrow density.

Investigating counts of attending adults as a means of censusing burrow-nesting puffins, Cairns (1979) reported error rates of 43% after 10 within-season replicate counts, and concluded that counts of attending puffins were of little use as indicators of population size. Thus, these methods are likely less reliable indicators of population change than the comparative colony-wide censuses conducted in 1979 and 1993-1994. Also, our exploration showed that the "Main colony" study area used by Nettleship to monitor attendance has been partially abandoned by the puffins. This may have contributed to apparent declines in attending adults.

For future surveys, we recommend that occupancy rates be determined early in the breeding season (i.e., during incubation) and that timing be standardized so that comparisons between years, habitats, or other factors are not confounded by differences in breeding success. Although burrow density estimates were almost identical in 1979 and 1993-1994, the use of more frequent, smaller quadrats in this study resulted in much narrower confidence limits than in 1979, and is recommended for future monitoring.

Population estimates for the puffin colonies on Gull and Green islands within the Witless Bay Seabird Ecological Reserve also were made in 1979 (Cairns and Verspoor 1980*; Nettleship, unpublished data). If we assume that the relative populations of the three Witless Bay islands have remained constant since 1979, our 1994 estimate for Great Island suggests a total population then of 200 000 – 230 000 pairs for the three colonies combined.

The total North American population of Atlantic Puffins is estimated to be in the region of 350 000 - 400 000 pairs (Chardine 1999*), of which over half

(54-62%) breed on the three main islands in the vicinity of Witless Bay, Newfoundland. As an indication of the importance of Great Island on a continental scale, about 30% of North American Atlantic Puffins breed at this location. Clearly then, the fate of North American Atlantic Puffins rests significantly on the future well-being of the Witless Bay colonies and on Great Island in particular.

Acknowledgments

We are grateful to Tommy, Marie, and John Reddick of Bauline East, Newfoundland, who provided transport to and from Great Island, maintained communication links while MSR and HMR were there, and have helped out in many ways over the years that Canadian Wildlife Service (CWS) and other personnel have worked on Great Island. Permission to work in the Witless Bay Seabird Ecological Reserve was granted by Department of Tourism, Culture and Recreation of the Government of Newfoundland and Labrador, and we thank Don Hustins, Glen Ryan and Doug Ballam for their assistance in this regard. Thank to CWS Pacific and Yukon Region for allowing us the use of their polar planimeter. We are grateful to David Cairns, John Coulson, Richard Elliot, Anthony Erskine, Tony Gaston, Mike Harris, and David Nettleship for valuable comments on previous versions of the manuscript, and to G. John Smith for reviewing the statistical content of the paper.

Documents Cited (marked by an asterisk in text)

Cairns, D. K., and **E. Verspoor.** 1980. Surveys of Newfoundland seabird colonies in 1979. Canadian Wildlife Service Report, Sackville, New Brunswick.

Chardine, J. W. 1999. Population status and trends of the Atlantic Puffin in North America. Bird Trends (7): 15–17. Canadian Wildlife Service, Ottawa.

Nettleship, D. N., J. W. Chardine, and **W. D. Lidster**. 1989. Monitoring numbers of Atlantic Puffins at Great Island, Newfoundland, 1968-1988. Canadian Wildlife Service Report, Dartmouth, Nova Scotia.

Rodway, M. S., H. M. Regehr, and **J. W. Chardine**. 1996. Population census of breeding Atlantic Puffins at Great Island, Newfoundland in 1993-94. Technical Report Series Number 263. Environmental Conservation Branch, Canadian Wildlife Service, Atlantic Region, Sackville, New Brunswick.

Literature Cited

Anker-Nilssen, T., and **O. W. Røstad**. 1993. Census and monitoring of Puffins *Fratercula arctica* on Røst, N Norway, 1979-1988. Ornis Scandinavica 24: 1–9.

Ashcroft, R. E. 1979. Survival rates and breeding biology of puffins on Skomer Island, Wales. Ornis Scandinavica 10: 100–110.

Bent, A. C. 1919. Life histories of North American diving birds. U.S. National Museum Bulletin 107: 1–239.

Bibby, C. J., N. D. Burgess, and **D. A. Hill**. 1992. Bird census techniques. Academic Press, London.

Cairns, D. 1979. Censusing hole-nesting auks by visual counts. Bird-banding 50: 358–364.

Cairns, D. K., W. A. Montevecchi, and **W. Threlfall**. 1989. Researcher's guide to Newfoundland seabird colonies. Memorial University of Newfoundland Occasional Papers in Biology Number 14.

Chapdelaine, G. 1995. Fourteenth census of seabird populations in the sanctuaries of the North Shore of the Gulf of St. Lawrence, 1993. Canadian Field-Naturalist 109: 220–226.

Drury, W. H. 1973-1974. Population changes in New England seabirds. Bird-Banding 44: 267-313; 45: 1–15.

Evans, P. G. H. 1980. Auk censusing manual. British Seabird Group, Tring, Hertfordshire.

Harris, M. P. 1984. The Puffin. T & A D Poyser, Calton.

Harris, M. P., and **S. Murray**. 1981. Monitoring of puffin numbers at Scottish colonies. Bird Study 28: 15–20.

Madow, W. G. 1953. On the theory of systematic sampling, III. Comparison of centered start and random start systematic sampling. Annals of Mathematical Statistics 24: 101–106.

Nettleship, D. N. 1972. Breeding success of the Common Puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. Ecological Monographs 42: 239–268.

Nettleship, D. N. 1976. Census techniques for seabirds of Arctic and eastern Canada. Canadian Wildlife Service Occasional Paper 25.

Nettleship, D. N. 1996. Family Alcidae (Auks). Pages 678-722 *in* Handbook of the Birds of the World, Volume 3: Hoatzin to Auks. *Edited by* J. del Hoyo, A. Elliot and J. Sargatal. Lynx Edicions, Barcelona.

Nettleship, D. N., and **P. G. H. Evans**. 1985. Distribution and status of the Atlantic Alcidae. Pages 53-154 *in* The Atlantic Alcidae. *Edited by* D. N. Nettleship and T. R. Birkhead. Academic Press, London.

Pennycuick, C. J., and **N. C. Kline**. 1986. Units of measurement for fractal extent, applied to the coastal distribution of bald eagle nests in the Aleutian Islands, Alaska. Oecologia 68: 254–258.

Rice, J. 1985. Interactions of variation in food supply and kleptoparasitism levels on the reproductive success of Common Puffins (*Fratercula arctica*). Canadian Journal of Zoology 63: 2743–2747.

Rodway, M. S., and **W. A. Montevecchi**. 1996. Sampling methods for assessing the diets of Atlantic Puffin chicks. Marine Ecology Progress Series 144: 41–55.

Rodway, M. S., J. W. Chardine, and **W. A. Montevecchi**. 1998. Intra-colony variation in breeding performance of Atlantic Puffins. Colonial Waterbirds 21: 171–184.

Received 20 April 2001
Accepted 31 March 2003

Response of Male Mountain Chickadees, *Poecile gambeli,* to Playback of Different Song Types

Myra O. Wiebe[1] and M. Ross Lein[2]

Department of Biological Sciences, University of Calgary, Calgary, Alberta T2N 1N4 Canada
[1]Present Address: Canadian Wildlife Service, 5204 50th Avenue, Suite 301, Yellowknife, Northwest Territories X1A 1E2 Canada
[2]Corresponding author: e-mail: mrlein@ucalgary.ca

Wiebe, Myra O., and M. Ross Lein. 2003. Response of male Mountain Chickadees, *Poecile gambeli,* to playback of different song types. Canadian Field-Naturalist 117(1): 76–81.

Individual male Mountain Chickadees (*Poecile gambeli*) have repertoires of 4-7 song types that vary in number and pitch of notes. Males sing different song types in different situations, suggesting that song types carry different behavioral messages. Using playback experiments conducted in the field, we measured the responses of male Mountain Chickadees to song types that differed in number and pitch of notes. Males responded similarly to playback of both common 3-note songs and common 2-note songs, so it is unclear whether these song types carry different messages. Males were more likely to approach the speaker during playback of descending 3-note songs (where each successive note is of lower pitch) than during playback of common 3-note songs (with the last two notes of the same pitch but lower-pitched than the first note). This supports our previous finding that these 3-note song types carry messages indicating different levels of aggression.

Key Words: Mountain Chickadee, *Poecile gambeli*, song repertoires, playback experiment, Alberta

In many bird species, variation in songs within an individual takes the form of a number of discrete categories of songs, or song types. Individual male Mountain Chickadees (*Poecile gambeli*) have song repertoires of 4-7 song types that vary in the number and pitch of notes (Wiebe and Lein 1999). Previously, we described the use of different song types by Mountain Chickadees in southwestern Alberta, Canada (Wiebe and Lein 1999). The three major song types were: "common 2-note song", with the second whistled note lower-pitched than the first whistled note; "common 3-note song", with the last two whistled notes of the same pitch but lower-pitched than the first whistled note; and "descending 3-note song", with each successive whistled note lower-pitched than the previous whistled note (Figure 1). Males used 3-note songs predominantly during undisturbed singing and 2-note songs predominantly during non-aggressive activity. Descending 3-note songs were associated with male-male interactions.

The objective of the present study was to test the response of male Mountain Chickadees to different song types, using song playback in the field to simulate a natural situation of a rival singing on another male's territory. One playback experiment ("note-number experiment") examined the effect of the number of notes by comparing responses to common 2-note songs versus common 3-note songs. A second experiment ("pitch experiment") examined the effect of pitch by comparing responses of males to common 3-note songs versus descending 3-note songs. Different song types were associated with different situations and may therefore carry different messages (Wiebe and Lein 1999). Assuming that song types with different messages elicit different responses from receivers, we predicted that males would respond differently to playback of different song types.

Methods

The study was conducted at the Barrier Lake site of the University of Calgary's Kananaskis Field Stations (51°00'N, 115°00'W) in the Kananaskis Valley in southwestern Alberta, Canada. Mountain Chickadees in this area inhabit forests dominated by Trembling Aspen (*Populus tremuloides*), White Spruce (*Picea glauca*), and Lodgepole Pine (*Pinus contorta*) (Wiebe 1995). Breeding pairs are monogamous and have territories of approximately 7 ha (Hill and Lein 1989a), which is relatively large for a small bird. Nests are in pre-existing cavities such as natural crevices or deserted nests of other cavity-nesting birds (Wiebe 1995).

Experimental Design of Playback Experiments

The subjects were 12 breeding male Mountain Chickadees. Because of their large territories, Mountain Chickadees are often difficult to locate when they are not singing, except during incubation or nestling stages, when the pair is usually around the nest site. Consequently, all playbacks were performed near the nest site during either of these stages so that the exact location of the male could be known at the start of the experiment. Many subjects and/or their mates were color-banded, allowing us to determine that the male was near enough to the nest to start the experiment. For pairs in which neither the

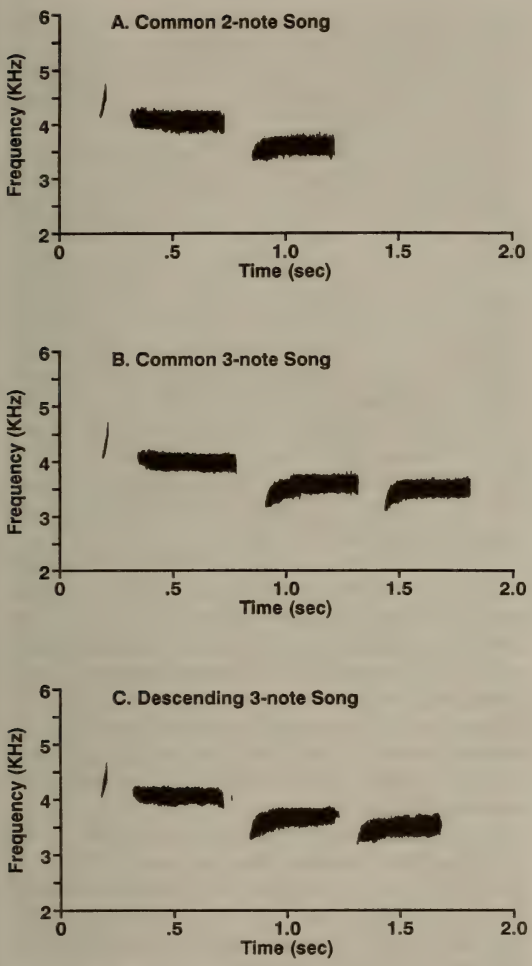


FIGURE 1. Examples of song types of Mountain Chickadees used in playback experiments. Song types were designated by the number and pitch of whistled notes. The brief introductory element, which is inaudible at a distance, was not counted in designating songs as "2-note", "3-note", etc.

male nor female was color-banded, we waited until both members of the pair were by the nest before starting the playback.

All playbacks were performed between 1 June and 18 June 1994 and were conducted between 05:00 and 12:00 (MST). Each male was used in both playback experiments, except for one male whose nest failed before the second experiment could be performed. We randomly determined which experiment was done first for each subject. The second experiment for a subject was conducted at least one week after the first to minimize any possible influence that the first playback might have had on the subject.

Each experimental session consisted of two trials. In the note-number experiment, one trial consisted of playback of common 2-note songs and the other consisted of playback of common 3-note songs. Similarly, in the pitch experiment, one trial consisted of playback of common 3-note songs and the other consisted of playback of descending 3-note songs. The presentation sequence of the two trials was randomized among subjects to control for order effects.

Construction of Playback Tapes

Playback tapes were made from songs recorded in 1993 and 1994 using Sony TCM-5000, Sony TCM-5000EV, or Stellavox SR-8 tape recorders. We prepared four playback tapes for each song type, each with a song from a different male. Two tapes were made from songs recorded in the one section of the study area and two were made from songs recorded in another section. To ensure that none of the subjects would be familiar with the playback songs, birds resident in one section were exposed to songs recorded from the other section. There was no movement of birds between these two sections during the breeding season, so it was unlikely that the subjects would have heard these songs previously. Furthermore, Mountain Chickadees usually breed on the same territory each year (personal observation), so it is improbable that songs recorded in 1993 could have been from former neighbors of any subject. We randomly chose which of the two tapes from the other area was to be used for each subject to prevent any biases in tape-selection.

SIGNAL bioacoustical analysis software (Engineering Design, Belmont, MA) was used to make playback tapes. Sound energy in songs of Mountain Chickadees ranges from 3000-4800 Hz, so we removed background noise below 2000 Hz and above 5000 Hz with a band-pass filter before capturing stimulus songs as digital sound files with SIGNAL. Using SIGNAL, stimulus songs were re-recorded onto cassette tapes at a rate of 10 songs/minute for a total of 3 minutes. The song rate of 10 songs/minute approximates that of a strongly singing male (personal observation).

Experimental Procedure During Playback Trials

Playbacks used a Sony TCM-5000EV cassette recorder, a custom-built, battery-powered amplifier, and an omnidirectional University Sound speaker. Playback volume was standardized at 68-71 dB, measured with a Realistic sound level meter (Model 42-3019) at 3 m from the speaker. This matched (by ear) the volume of songs of a strongly singing male. Following the methodology of Hill and Lein (1989b), the speaker was suspended in a tree 15 m from the nest in the direction of the nearest territorial boundary, at a height of 1.5-2.1 m above the ground. Four rows of small flags radiating at 90° angles were placed at distances of 5 m and 10 m from the speaker to aid in estimation of the subject's distance from the speaker.

Trials started when the subject was within 10 m of the nest cavity and was engaged in non-aggressive

activity such as feeding the female or nestlings. As well, trials started only if no songs from the male or a neighbor had been heard during the previous 10 minutes. Each trial consisted of a 3-minute test period when the tape was played and a 3-minute post-test silent period. Mountain Chickadees return to pre-playback behavior in less than 10 minutes after a playback trial (Hill and Lein 1989b), so we waited 10 minutes or more before starting the second trial in each experimental session.

We used two observers, located on opposite sides of the speaker and 10 m from it, during the playbacks because it was sometimes difficult to see the subject in areas of dense vegetation. One observer used a Sony TCM-5000 cassette recorder, Sony PBR-330 parabolic reflector, and AKG D190E microphone to record all vocalizations given by the subject and to record an oral description of the subject's location relative to the speaker. The second observer used a Sony TCM-5000EV or Sony TC-142 cassette recorder and a Sony ECM-95S microphone to record an oral description of the subject's location and behavior. Both observers noted when the male was within 5 m or 10 m of the speaker. As well, the number of flights over the speaker and the closest vertical and horizontal approach of the bird to the speaker were estimated during the trial. The playback songs could be heard on the dictated recordings of both observers, permitting the two recordings to be synchronized during analysis.

Data Analysis

The OBSERVER computer program (Noldus Information Technology, Wageningen, The Netherlands) was used to transcribe recordings made during playback. We chose response variables similar to those used as indicators of response in previous playback experiments with chickadees (e.g. Hill and Lein 1989b; Lohr et al. 1994). The response variables measured were (1) closest horizontal approach to speaker in metres; (2) closest vertical approach to speaker within a horizontal distance of 10 m; (3) latency of first approach within a horizontal distance of 10 m of speaker in seconds; (4) time spent 0-5 m from speaker in seconds; (5) time spent 5-10 m from speaker in seconds; (6) number of flights over speaker; (7) number of gargle calls; (8) latency of first song in seconds; (9) total number of songs; (10) number of common 2-note songs; (11) number of common 3-note songs; and (12) number of descending 3-note songs. If a subject did not approach within 10 m of the speaker during the entire trial, we assigned maximum values for latency of first approach (360 s), closest vertical approach (12 m) and closest horizontal approach (10 m).

Using two-sample t-tests comparing each response variable for each playback stimulus we determined whether breeding stage (incubation vs. nestling) of subjects influenced response to playback. We also conducted similar tests with each playback stimulus to determine whether the presentation sequence of the trials within an experiment or the order in which the two experiments were performed affected responses of subjects.

We compared the responses of males to playback of different song types using a combination of multivariate and univariate statistics. Principal components analysis is appropriate for playback data in which many response variables are likely to be interrelated and when clarity is difficult to maintain if all original variables are presented (McGregor 1992). We measured responses of males to playback by calculating principal component scores for each male during each trial and compared these new variables with paired t-tests. We followed the approach of McGregor (1992), in which a single principal components analysis was done for both experiments. We use the term "response factors" to refer to the principal components.

All variables were used for principal components analysis except those for which response was influenced by the presentation sequence of the trials, and numbers of songs of different types. We omitted numbers of songs of different types because, if song types did have the same messages, then a difference in numbers of songs of a particular type would not indicate a stronger response. Instead, we compared numbers of songs of different type in a separate analysis using paired t-tests.

All playback experiments were included in the analysis. Most statistical analyses were done using STATISTIX 3.5 (Analytical Software, St. Paul, MN) with an alpha level of 0.05. All statistical tests are two-tailed. Tests of statistical power used the procedure outlined by Cohen (1977).

Results

Almost all subjects showed some response to song playback during the experiments. Most subjects approached the speaker during the song playback, and many sang during the playback or post-playback periods. Some flew over the speaker during playback and a few individuals gave "gargle" calls, which are short-distance aggressive calls (Gaddis 1985). Appendix 1 gives means and standard errors for response variables during the entire 6-minute trial of playback experiments.

Response of subjects did not differ significantly between breeding stages or with the order in which the two experiments were conducted. In addition, most response variables did not differ significantly between the two presentation sequences of trials within an experiment. However, in the note-number experiment, subjects had a significantly shorter latency of first song if playback of common 2-note songs was the first trial of the experiment rather than the second ($n = 11$, unequal variances, df = 8.1,

$t = -4.61$, $P < 0.002$). Similarly, in the pitch experiment, the closest horizontal approach distance was significantly smaller if playback of descending 3-note songs was the first trial rather than the second ($n = 12$, unequal variances, df = 6.0, $t = -2.46$, $P < 0.05$). Because of the possible influence of presentation order, we eliminated these two variables from subsequent analyses.

Principal Components Analysis

For principal components analysis to be a useful technique, the original variables must show some correlation. If they are not correlated, or only weakly correlated, principal components analysis will simply select them in order of variability (McGregor 1992). The variables used in the principal components analysis were correlated: more than half of the values in the correlation matrix were > 0.2. No variable had more than two correlation values < 0.1.

Principal components analysis of the seven response variables extracted three factors with eigenvalues ≥ 1.0 that accounted for 75.7% of the variance in response (Table 1). We considered response variables with correlations (factor loadings) >0.4 to be important for a particular response factor.

Variables related to approach to the speaker (closest approach, latency of approach, time spent 0-5 m from speaker) were highly correlated with the first response factor (Table 1; "Approach" factor). Subjects with high scores on this factor approached the speaker more than did those subjects with low scores. Variables related to distance from the speaker (time spent 0-5 from speaker, time spent 5-10 m from speaker, flights over speaker) and aggressive vocalizations (gargles) were highly correlated with the second response factor (Table 1; "Movement/Gargles factor"). High scores on this factor indicate that subjects spent more time near the speaker and gave many gargles, whereas low scores indicate that the subjects spent more time mid-distance from the speaker and flew over the speaker more frequently. The number of songs given was the only variable that was highly correlated with the third response factor (Table 1; "Song factor"). High scores on this factor indicate that the subjects sang frequently during the experiment.

In the note-number experiment, males were more likely to approach the speaker (i.e., higher approach factor scores) during the playback of common 3-note songs than during the playback of common 2-note songs, but this difference was not statistically significant (Table 2). However, the statistical power of this comparison was only 38.5% ($n = 11$, $\alpha = 0.05$). There was no significant difference in response for either the movement/gargle factor or the song factor when the playbacks of common 2-note songs and common 3-note songs were compared (Table 2). Both these comparisons also had very low statistical power (< 10.0% ; $n = 11$, $\alpha = 0.05$).

In the pitch experiment, males were significantly more likely to approach the speaker during playback of descending 3-note songs than during playback of common 3-note songs (Table 2). There was no significant difference in scores on either the movement/gargle or song factors between playbacks of descending 3-note songs and common 3-note songs (Table 2), but the statistical power of these tests was low (< 14.0%; $n = 12$, $\alpha = 0.05$).

During some trials with playback of descending 3-note songs, songs of responding males duplicated the pitch of the notes in the playback songs almost perfectly, suggesting that they might be "matching" the stimulus song. However, the number of each song type that males sang during playback trials did not significantly differ between trials in either playback experiment (paired t-tests, $P \geq 0.10$).

TABLE 1. Correlations of response variables with the first three response factors obtained in principal components analysis of responses of male Mountain Chickadees to song playback. Correlation coefficients (factor loadings) > 0.4 have been italicized to indicate variables that accounted for most of the variation in the response factor.

Response Variable	Response Factor		
	Approach	Movement/Gargles	Song
Closest vertical approach	*- 0.54*	0.04	0.12
Latency of approach	*- 0.48*	0.04	0.25
Time 0-5 m from speaker	*0.42*	*0.45*	- 0.09
Time 5-10 m from speaker	0.21	*- 0.58*	- 0.15
Number of flights over speaker	0.38	*- 0.44*	0.21
Number of gargles	0.27	*0.50*	- 0.00
Number of songs	0.19	0.04	*0.92*
Eigenvalue	2.59	1.71	1.00
% variance explained	37.0%	24.4%	14.3%

TABLE 2. Comparison of scores (mean ± SE) of subjects on the three response factors for the entire 6-minute trial of playback. *P*-values are for 2-tailed, paired t-tests comparing the pair of means immediately above the *P*-value.

	Playback Experiment			
	Note-Number (n = 11)		Pitch (n = 12)	
Response Factor	Common 2-note	Common 3-note	Common 3-note	Descending 3-note
Approach	- 0.45 ±0.4	0.41 ± 0.5	- 0.64 ± 0.4	0.68 ± 0.5
	P = 0.11		P = 0.03	
Movement/gargles	- 0.16 ± 0.3	0.17 ± 0.5	0.08 ± 0.3	- 0.08 ± 0.5
	P = 0.55		P = 0.75	
Song	0.13 ± 0.3	0.01 ± 0.3	- 0.23 ± 0.2	0.10 ± 0.3
	P = 0.80		P = 0.39	

Discussion

Males did not respond differently to playback of common 2-note songs and common 3-note songs. Observational data showed that these two song types were used in different situations and hence may have different messages (Wiebe and Lein 1999), so the lack of any significant differences in response is contrary to predictions. Males of some other species did not respond differently to playback of different song types (e.g., Martin 1980; Searcy et al. 1982), suggesting that song types in these species probably convey similar messages, at least during male-male interactions. However, the statistical power of our test was low, implying a high probability of committing a Type II error. Clearly, more experimental work, with a larger sample size, needs to be done before the null hypothesis can be accepted or rejected with any certainty.

Our finding that males were more likely to approach playback of descending 3-note songs than common 3-note songs agrees with the prediction that males would respond differently to these two song types, and supports our previous suggestion (Wiebe and Lein 1999) that these song types carry different messages indicating different levels of aggression. We argued that descending 3-note songs convey more aggressive messages than do common 3-note songs. The fact that males responded more to playback of a song type used in male-male interactions (descending 3-note songs), than to a song type used in undisturbed territorial advertisement (common 3-note songs) (Wiebe and Lein 1999), is comparable to some studies of other species that showed a stronger response to a song type judged to carry a more aggressive message (Ficken and Ficken 1970; Nelson and Croner 1991). However, other species have shown a reduced response to playback of song types judged to be more aggressive (Järvi et al. 1980; Catchpole 1983).

Males of some species match song types as a method of directing their songs to particular singing rivals (Falls et al. 1982). Although some males in our study seemed to be song-matching by sometimes copying the exact pitch of stimulus songs during the descending 3-note trial, we did not find any relationship between the numbers of each song type sung by males during a trial and the stimulus song type. Further tests using interactive playback experiments (Dabelsteen 1992) may be useful to determine if song-matching occurs in Mountain Chickadees or if males seemed to match the stimulus song type merely because their descending 3-note songs resembled the stimulus song by chance.

Acknowledgments

We thank S. R. M. Shima for her able assistance throughout the field work. J. Day, S. Vandervaart, and K. Frankowski also assisted with field work. G. Chilton provided help and advice during various stages of the project. The staff at the Barrier Lake site of the University of Calgary's Kananaskis Field Stations provided support and accommodation during the field season. R. M. R. Barclay, A. P. Russell, and P. Asquith gave constructive comments on earlier drafts of the manuscript. This project was supported by research assistantships from the University of Calgary to MOW and a research grant from the Natural Sciences and Engineering Research Council of Canada to MRL.

Literature Cited

Catchpole, C. K. 1983. Variation in the song of the Great Reed Warbler *Acrocephalus arundinaceus* in relation to mate attraction and territorial defense. Animal Behaviour 31: 1217–1225.

Cohen, J. 1977. Statistical power analysis for the behavioral sciences. Academic Press, New York.

Dabelsteen, T. 1992. Interactive playback: a finely tuned response. Pages 97-109 *in* Playback and studies of animal communication. *Edited by* P. K. McGregor. NATO ASI Series A, Volume 228. Plenum Press, New York.

Falls, J. B., J. R. Krebs, and **P. K. McGregor.** 1982. Song matching in the Great Tit (*Parus major*): the effect of similarity and familiarity. Animal Behaviour 30: 997–1009.

Ficken, M. S., and **R. W. Ficken.** 1970. Responses of four warbler species to playback of their two song types. Auk 87: 296–304.

Gaddis, P. K. 1985. Structure and variability in the vocal repertoire of the Mountain Chickadee. Wilson Bulletin 97: 30–46.

Hill, B. G., and **M. R. Lein.** 1989a. Territory overlap and habitat use of sympatric chickadees. Auk 106: 259–268.

Hill, B. G., and **M. R. Lein.** 1989b. Natural and simulated encounters between sympatric Black-capped Chickadees and Mountain Chickadees. Auk 106: 645–652.

Järvi T., T. Radesäter, and **S. Jakobsson.** 1980. The song of the Willow Warbler *Phylloscopus trochilus* with special reference to singing behaviour in agonistic situations. Ornis Scandinavica 11: 236–242.

Lohr, B., R. Weisman, and **S. Nowicki.** 1994. The role of pitch cues in song recognition by Carolina Chickadees (*Parus carolinensis*). Behaviour 130: 1–15.

Martin, D. J. 1980. Response by male Fox Sparrows to broadcast of particular conspecific songs. Wilson Bulletin 92: 21–32.

McGregor, P. K. 1992. Quantifying responses to playback: one, many, or composite multivariate measures? Pages 79-96 *in* Playback and studies of animal communication. *Edited by* P. K. McGregor. NATO ASI Series A, Volume 228. Plenum Press, New York.

Nelson, D. A., and **L. J. Croner.** 1991. Song categories and their functions in the Field Sparrow (*Spizella pusilla*). Auk 108: 42–52.

Searcy, W. A., M. H. Searcy, and **P. Marler.** 1982. The response of Swamp Sparrows to acoustically distinct song types. Behaviour 80: 70–83.

Wiebe, M. O. 1995. The function of song types in the Mountain Chickadee (*Parus gambeli*). M.Sc. thesis, University of Calgary, Calgary, Alberta, Canada.

Wiebe, M. O., and **M. R. Lein.** 1999. Use of song types by Mountain Chickadees (*Poecile gambeli*). Wilson Bulletin 111: 368–375.

Received 12 February 2001
Accepted 20 May 2003

APPENDIX 1. Response variables for subjects (mean ± SE) during the entire 6-minute trial of playback experiments.

	Playback Experiment			
	Note-Number (n = 11)		Pitch (n = 12)	
Response Variable	Common 2-note	Common 3-note	Common 3-note	Descending 3-note
Closest horizontal approach (m)	4.4 ± 1.4	2.0 ± 0.9	3.1 ± 1.3	1.7 ± 0.9
Closest vertical approach (m)	8.2 ± 1.2	5.1 ± 1.4	8.1 ± 1.0	5.3 ± 0.9
Latency of approach (s)	136.1 ± 34.7	81.4 ± 32.4	144.6 ± 39.3	73.7 ± 28.8
Time 0-5 m from speaker (s)	89.6 ± 33.0	123.5 ± 33.1	100.3 ± 32.8	139.9 ± 41.4
Time 5-10 m from speaker (s)	58.0 ± 16	4 42.9 ± 14.2	38.3 ± 12.8	53.3 ± 14.9
No. of flights over speaker	0.4 ± 0.2	0.8 ± 0.3	0.4 ± 0.3	1.1 ± 0.5
No. of gargles	0.0 ±0.0	0.4 ± 0.4	0.0 ± 0.0	0.3 ± 0.3
Latency of first song (s)	192.5 ± 46.2	203.5 ± 47.3	229.1 ± 44.6	148.3 ± 43.3
Total number of songs	12.7 ± 4.5	12.0 ± 5.1	5.9 ± 2.6	13.8 ± 4.3

Are There Two Species of Pygmy Shrews *(Sorex)*? Revisiting the Question Using DNA Sequence Data

DONALD T. STEWART[1], MICHELLE MCPHERSON[1], JODY ROBICHAUD[1] and LUCA FUMAGALLI[2]

[1]Biology Department, Acadia University, Wolfville, Nova Scotia B4P 2R6 Canada
[2]Institut d'Ecologie, Laboratoire de Biologie de la Conservation, Bâtiment de Biologie, Université de Lausanne, CH-1015, Lausanne, Switzerland

Stewart, Donald T., Michelle McPherson, Jody Robichaud, and Luca Fumagalli. 2003. Are there two species of Pygmy Shrews *(Sorex)*? Revisiting the question using DNA sequence data. Canadian Field-Naturalist 117(1): 82–88.

Pygmy Shrews in North America have variously been considered to be one species (*Sorex hoyi*) or two species (*S. hoyi* and *S. thompsoni*). Currently, only *S. hoyi* is recognized. In this study, we examine mitochondrial DNA sequence data for the cytochrome *b* gene to evaluate the level of differentiation and phylogeographic relationships among eleven samples of Pygmy Shrews from across Canada. Pygmy Shrews from eastern Canada (i.e., Ontario, Quebec, New Brunswick, Nova Scotia, and Prince Edward Island) are distinct from Pygmy Shrews from western Canada (Alberta, Yukon) and Alaska. The average level of sequence divergence between these clades (3.3%) falls within the range of values for other recognized pairs of sister species of shrews. A molecular clock based on third position transversion substitutions suggests that these two lineages diverged between 0.44 and 1.67 million years ago. These molecular phylogenetic data, combined with a re-interpretation of previously published morphological data, are suggestive of separate species status for *S. hoyi* and *S. thompsoni* as has been previously argued by others. Further analysis of specimens from geographically intermediate areas (e.g., Manitoba, northern Ontario) is required to determine if there is secondary contact and/or introgression between these two putative species.

Key Words: Pygmy Shrew, *Sorex hoyi*, Thompson's Pygmy Shrew, *S. thompsoni*, molecular systematics, cytochrome *b*.

In various treatments of North American shrews over the years, two points regarding Pygmy Shrew taxonomy have been particularly problematic. The first relates to their generic or subgeneric status. The second issue is whether there is more than one species of Pygmy Shrew in North America. The first question has been addressed most recently by George (1988), Stewart and Baker (1994), and Fumagalli et al. (1999). Although there now appears to be a consensus that Pygmy Shrews belong in the subgenus *Otisorex* (e.g., Hutterer 1993), the specific relationship of Pygmy Shrews to other *Otisorex* shrews is not clear. For example, no clear sister-group relationship for Pygmy Shrews emerged from the allozyme work of George (1988). Stewart and Baker (1994) analysed partial mtDNA D-loop region sequences and found Pygmy Shrews to be affiliated with Water (*Sorex palustris*), Dusky (*S. monticolus*) and Vagrant Shrews (*S. vagrans*). Fumagalli et al. (1999), however, failed to resolve interspecific relationships of North American Pygmy Shrews to other members of the *Otisorex*.

With regard to the second point raised above, Hutterer (1993) recognized only one species of North American Pygmy Shrew, *Sorex hoyi*. Hutterer's decision was based in part on the multivariate, morphological work of van Zyll de Jong (1976) and Diersing (1980). Van Zyll de Jong (1976) was particularly interested in whether there was support for recognizing *S. thompsoni* as a separate species from *S. hoyi* as proposed by Long (1972, 1974). "*S. thompsoni*" (including *S. h. thompsoni* + *S. h. winnemana*) is generally described as a smaller form with a relatively long tail and is found throughout eastern Canada, New England, New York State, and the Appalachian Mountains as far south as Georgia. *S. h. hoyi*, the most widespread of the recognized subspecies, is somewhat larger and occurs across Canada from Labrador to the Rocky Mountains and north to the Yukon Territories.

Van Zyll de Jong (1976) concluded that there was sufficient overlap in morphological variation that all forms, including *S. thompsoni*, be recognized as subspecies of *S. hoyi*. Diersing (1980) examined 21 cranial characters for over 400 specimens of Pygmy Shrews representing five putative subspecies (*S. h. hoyi, S. h. eximius, S. h. montanus, S. h. winnemana,* and *S. h. thompsoni*). Although a two-dimesional principal component plot indicated some differentiation among these five forms, he concluded that there is intergradation or sufficient morphological similarity among the forms that they should be be recognized as subspecies rather than distinct species.

The exact ranges of two of these taxa, *S. h. thompsoni* and *S. h. hoyi,* has also been the subject of some debate. Long (1972) suggested that Pygmy Shrews from the Gaspé Peninsula, Quebec, were more similar to shrews on the north side of the St. Lawrence River than they were to contiguous populations from New Brunswick. Van Zyll de Jong (1976) initially followed this split (although he later combined the Gaspé population with all populations east of the St. Lawrence; van Zyll de Jong 1983). In contrast,

Diersing (1980) combined shrews from the Gaspé with *S. h. thompsoni* but he also included some populations of shrews from southern Ontario and southeastern Quebec in this subspecies.

Given the history of controversy involving the Pygmy Shrew, and given the recent demonstration of significant genetic differentiation among morphologically similar taxa in the Dusky Shrew complex, *Sorex monticolus* and relatives (Demboski and Cook 2001), the Arctic Shrew (*Sorex arcticus/ S. maritimensis*) complex (Stewart et al. 2002), and various Eurasian species (reviewed in Fumagalli et al. 1999), it was our objective to use molecular data to revisit the question asked by van Zyll de Jong (1976), "Are there two species of Pygmy Shrews?"

Methods

Specimens and sample preparation

Pygmy Shrews were collected from various sites across Canada (Figure 1 and Table 1): Seebe, Alberta; Toronto and Gogama, Ontario; Sept-Îsles, Quebec; Edmundston, New Brunswick; Hope River, Prince Edward Island; and Windsor, Nova Scotia. All shrews were collected in pitfall traps and either dissected immediately or frozen whole in liquid nitrogen. Total DNA was extracted from various organ tissues using a standard phenol-chloroform isolation protocol. Partial cytochrome *b* sequences for two Pygmy Shrews specimens from the Yukon Territories, Canada (1011 bp) and Alaska, USA (672 bp), were also downloaded from the GenBank database for inclusion in the phylogenetic analysis. Cytochrome *b* is a mitochondrial DNA encoded gene that has been used extensively for phylogenetic analysis of closely related mammalian species including shrews (see Fumagalli et al. 1999; Demboski and Cook 2001). (Note: although additional sequence was available for the Alaska specimen, only 672 bp overlapped with the 1011 bp of *cyt b* data examined herein.) Several additional *cyt* b

Figure 1. Geographic range of North American Pygmy Shrew taxa and the locations sampled for this study. Ranges were derived from various published sources (Hall and Kelson 1959, Banfield 1974, Diersing 1980, van Zyll de Jong 1983) and are therefore only approximate: 1. *S. hoyi eximius*, 2. *S. hoyi washingtoni*, 3. *S. hoyi hoyi*, 4. *S. hoyi alnorum*, 5. *S. hoyi winnemana*, 6. *S. hoyi thompsoni*, and 7. *S. montanus*. Samples from this study that fall within the "Eastern Clade" (*S. thompsoni*) are marked with circles and samples that fall within the "Western Clade" are marked with triangles (see Figure 2).

TABLE 1. Collection locality, catalogue numbers and GenBank accession numbers for the Pygmy Shrew samples analyzed herein. "DTS" samples are part of the collection of the Royal Ontario Museum (ROM).

Taxonomy*	Clade	ROM Cat. No.	Collector Cat. No.	GenBank No.	Locality
S. h. thompsoni	"Eastern"	109915	DTS599	AY310337	Windsor, Nova Scotia (44°56'N 64°11'W)
S. h. thompsoni	"Eastern"	110061	DTS818	AY310338	Hope River, Prince Edward Is. (46°28'N 63°23'W)
S. h. thompsoni	"Eastern"	109467	DTS124	AY310340	Edmundston, New Brunswick (47°28'N 68°14'W)
S. h. thompsoni	"Eastern"	109487	DTS144	AY310341	Edmundston, New Brunswick (47°28'N 68°14'W)
S. h. thompsoni	"Eastern"	109686	DTS350	AY310342	Toronto, Ontario (43°56'N 79°32'W)
S. h. hoyi	"Eastern"	110177	DTS935	AY310344	Gogama, Ontario (47°40'N 81°43'W)
S. h. hoyi	"Eastern"	110249	DTS1016	AY310339	Sêpt Isles, Québec (50°12'N 66°23'W)
S. h. hoyi	"Western"	109728	DTS399	AY310336	Ghost River, Alberta (51° 17'N 114° 50'W)
S. h. hoyi	"Western"	109811	DTS494	AY310343	Seebe, Alberta (51° 6'N 115° 4'W)
S. h. hoyi	"Western"	Not Available	IZEA7†	AF238040	Ogilvie Mountains, Yukon (64°03'N 139°25'W)
S. h. eximius	"Western"	Not Available	AFTC7982‡	AJ000460	Hughes Quadrangle, Alaska (66°02'N 154°16'W)

*Putative taxonomic rank based on geographical patterns reported in Diersing (1980).
†See Fumagalli et al. (1999).
‡See Demboski and Cook (2001).

sequences for *Otisorex* shrews (two each from *S. monticolus, S. pacificus, S. palustris, S. cinereus, S. haydeni*) and two from *S. trowbridgii* were also included in the data set. These latter samples were previously analysed by Fumagalli et al. (1999) as part of a large-scale phylogenetic analysis of the genus *Sorex*.

Amplification and sequencing of cytochrome b.

Amplification and subsequent sequencing of the *cyt* b gene was performed using the primer pair CB1-5' and H15915 (Irwin et al. 1991; Palumbi 1996). PCR amplification parameters were as follows: 94°C denaturation for 30 s, 50°C annealing for 1 min, and a 72°C extension for 1.5 min. A total of 40 cycles was performed. PCR products were gel purified using a gel extraction kit (Qiagen) and 30-90 ng of cleaned DNA was sequenced in both directions on an Applied Biosystems 377 DNA sequencer. Sequences were aligned using ClustalW (Thompson et al. 1994).

Phylogenetic Analyses

Phylogenetic analysis was conducted using maximum parsimony (MP), maximum likelihood (ML), and neighbor-joining (NJ) methods in PAUP* 4.0b8 (Swofford 2000) and Mega 2 (Kumar et al. 2001). To determine the relationship between Pygmy Shrews and the other members of the subgenus *Otisorex, S. trowbridgii* was selected as an outgroup reference species based on the tree presented in Fumagalli et al. (1999). Two samples from each of the seven additional representative species listed above were included in the MP and NJ analyses. For the ML analysis, only one representative from each of these species was used to increase the efficiency of the search routine.

For the MP analyses, we implemented a heuristic search routine with 100 stepwise, random addition replicates with tree-bisection-reconnection branch swapping. Given that transition substitutions were approximately 4-5 times as common as transversions, we conducted a weighted parsimony analysis with a conservative TS:TV ratio set at 2. For the ML analysis, we implemented model parameters calculated for the most parsimonious tree inferred for this data set. For substitution rate parameters, the following values were used: AC = 3.7632, AG = 9.7588, AT = 2.4182, CG = 0.9840, and CT = 19.5223. For

the proportion of invariable sites, a value of 0.6059 was used and for τ shape parameter, a value of 2.919 was implemented. For the neighbor-joining analysis, a matrix of genetic distances based on Kimura's two-parameter estimates was used with missing data eliminated in pairwise comparisons only. Support for individual nodes under the MP and NJ analyses was evaluated using 1000 bootstrap replicates. For the ML analyses, 100 bootstrap replicates were performed.

Several additional analyses were conducted using the Mega 2 package (Kumar et al. 2001). Average pairwise distances between recognized clades of Pygmy Shrews were calculated using Kimura's two-parameter estimates. These clades were inferred from the phylogenetic trees generated using the aforementioned methods. Standard errors for these pairwise distance estimates were calculated using 500 bootstrap replicates. To date the time of divergence between these clades, we used the approach described in Fumagalli et al. (1999). Average between-group distances were calculated for third-position transversions, and these values, which have been shown to accumulate linearly though time (e.g., Irwin et al. 1991), were used to estimate the time of divergence of major lineages.

Results

Basic Sequence Statistics

A 1011 bp section of the cytochrome *b* gene was analysed for 11 specimens of Pygmy Shrews from across Canada and Alaska. Among the Pygmy Shrews alone, 58 (5.7%) sites were variable, of which 43 (4.3%) were parsimony informative. As was observed by Fumagalli et al. (1999), there is a nucleotide composition bias in that guanine constitutes only 14.8% of nucleotides. The other three nucleotides had similar frequencies: adenine (27.6%), cytosine (29.1%), and thymine (28.5%).

Phylogenetic relationships

Essentially the same tree was produced by each of the three phylogenetic methods (i.e., MP, ML, and NJ) and this tree is presented in Figure 2. The following four "major" clades were consistently returned with bootstrap support of 89-100% for each method: (1) Pygmy Shrews; (2) *S. fumeus*; (3) *S. haydeni* and *S. cinereus*; and (4) *S. monticolus*, *S. pacificus*, *S. palustris*, and *S. vagrans*. However, none of the methods used resolved the placement of Pygmy Shrews relative to the other members of the subgenus *Otisorex* (i.e., Pygmy Shrews were not clearly a sister-group to any of these other clades). Among Pygmy Shrews, all trees indicated two clades: an eastern Canadian clade consisting of samples from Ontario, Quebec, New Brunswick, Nova Scotia and Prince Edward Island, and a western North American clade consisting of specimens from Alberta, the Yukon and Alaska. While the eastern clade received consistently high bootstrap support (80-99%) by all methods, support for the western clade of Pygmy Shrews varied from moderate to high (59, 71, and 92% for the ML, MP and NJ analyses, respectively).

Distance estimates and divergence times

There were virtually no differences between the matrix of basic p-distances and the matrix of Kimura's two parameter estimates among the collection of Pygmy Shrews sampled from across Canada. The number of uncorrected nucleotide substitutions observed between samples of Pygmy Shrews for which the full 1011 bp of *cyt* b were available varied between 2 (i.e., p-distance = 0.002) for the two specimens from Edmundston, New Brunswick, and 43 (p=0.043) for the samples from the Ogilvie Mts., Yukon Territory, and Gogama, Ontario. All samples from different locations differed by at least 4 substitutions (p=0.004). The average number of Kimura's two-parameter differences between the eastern and western clades was 0.033±0.002 (3.3%). Average within group differences were considerably smaller. The average number of substitutions estimated using Kimura's two-parameter model was 0.013±0.002 for the eastern clade and 0.005±0.002 for the western clade.

For the purpose of estimating the time of divergence between these two clades of Pygmy Shrews, we estimated the number of third position transversion substitutions using Kimura's two parameter estimates and arrived at a value of 0.012±0.006 or 1.2±0.6%. Using a rate of sequence divergence calibrated for shrews at 1.36±0.28%/Myr (Fumagalli et al. 1999), this translates into an estimated time of divergence for these two lineages of 0.88 Myr or 880,000 yr ago. The 95% confidence interval for this divergence time was determined as follows. First we used the smaller divergence estimate (i.e., 1.2-0.6=0.6%) divided by the higher rate calibration (i.e., 1.36+0.28=1.64%/Myr) and arrived at a lower divergence time estimate of 0.44 Myr or 440,000 yr. We then used the larger divergence estimate (1.8%) divided by the smaller rate calibration (1.08%/Myr) and arrived at an upper divergence time estimate of 1.67 Myr ago.

Interspecific distance comparisons

To place the amount of sequence divergence observed between the two clades of Pygmy Shrews into context, we calculated the proportion of nucleotide substitutions (Kimura's two parameter estimates) between several recognized pairs of sister-species in the genus *Sorex*. These included the following pairs of species: *S. cinereus-S. haydeni* (d=8.3%), *S. monticolus-S. pacificus* (d=0.7%), *S. caecutiens-S. shinto* (d=9.3%), *S. araneus-S. granarius* (d=1.4%), and *S. tundrensis-S. asper* (d=5.5%). To summarize these data, interspecific distance estimates ranged from 0.7% to 9.3% with an average value of 5.0%. The amount of sequence

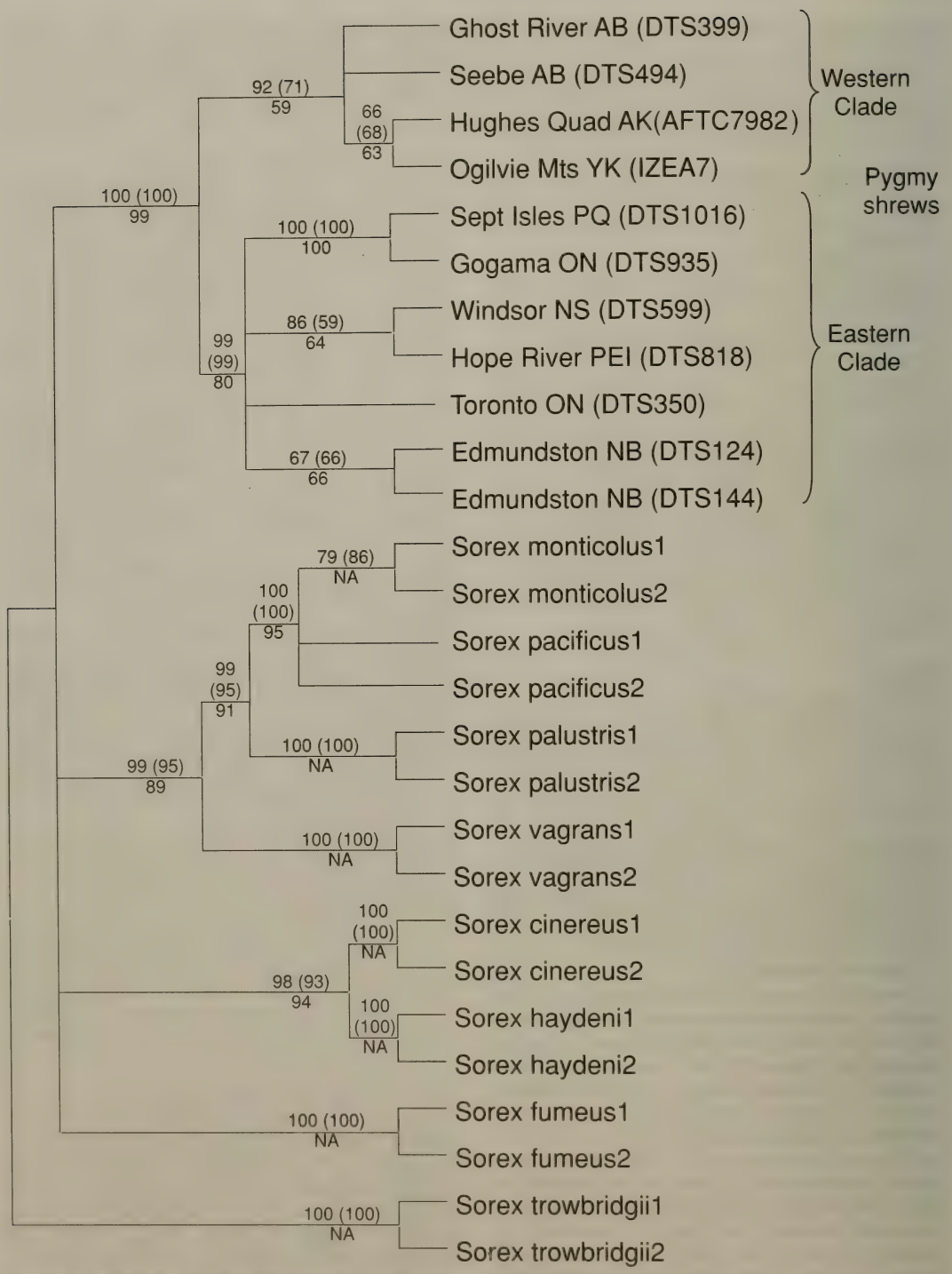


FIGURE 2. Consensus of the three bootstrap consensus trees produced by neighbor-joining (NJ), maximum parsimony (MP), and maximum likelihood (ML) methods. Refer to the text for details of the parameters used in each of these three methods. Bootstrap values for the NJ analysis are indicated above the branches, for MP the bootstrap values are shown in brackets, and the ML values are shown below the branch. Note that only one sample for each of the non-pygmy shrew species was included in the ML analysis so ML bootstrap values were not available for some branches (indicated NA on the tree). For the MP analysis, the most parsimonious tree had a length of 737 steps with a consistency index of 0.634. For the ML analysis, the best tree had –lnL=3872.9547.

divergence between the eastern and western clades of Pygmy Shrews was somewhat less than the average at 3.3%.

Discussion

Interspecific relationships

Stewart and Baker (1994) used partial control region sequences to reconstruct relationships among several species in the subgenus *Otisorex*. They found that Pygmy Shrews formed a sister group to a clade consisting of *S. monticolus, S. vagrans,* and *S. palustris* (but the ordering of these three species was not resolved). They also showed that *S. fumeus* formed a sister group to the *S. cinereus* complex. The phylogenetic analyses presented herein (Figure 2) mirrored some but not all of their findings. Essentially, the deeper branching pattern among (1) Pygmy Shrews, (2) the *S. cinereus* complex, (3) *S. fumeus,* and (4) *S. monticolus, S. pacificus, S. palustris,* and *S. vagrans* as presented herein is unresolved. As others have suggested (e.g., George 1988; Fumagalli et al. 1999; Demboski and Cook 2001; Stewart et al. 2002), this pattern indicates that North American shrews underwent a relatively rapid adaptive radiation during the late Pliocene or early Pleistocene.

Phylogenetic/phylogeographic relationships of Pygmy Shrews

In terms of intraspecific phylogenetic relationships, the tree presented herein (Figure 2) indicates moderate to strong support for distinct "eastern" and "western" clades of Pygmy Shrews. While the eastern clade was consistently well supported, only the NJ analysis provided particularly strong (i.e., 92%) support for the western clade as well. This may represent a difficulty in correctly rooting Pygmy Shrews to the remaining species included in the analysis. When only Pygmy Shrews were considered, the un-rooted network consistently separated eastern and western specimens in 100% of all bootstrapped replicates for all methods.

These observed clades correspond to some degree to the ranges of the subspecies *S. h. hoyi* ("western" clade) and *S. h. thompsoni* ("eastern" clade) as presently recognized (although the Alaska sample is within the range of the putative subspecies *S. h. eximius*). Several specific aspects of the phylogenetic relationships among the Pygmy Shrew samples examined herein are noteworthy. First, the samples from north of the St. Lawrence River-Great Lakes waterway are grouped with the samples from southeast of the St. Lawrence (i.e., the samples from New Brunswick, Prince Edward Island and Nova Scotia). This is partially consistent with the proposed range of *S. h. thompsoni* as described by Diersing (1980) and van Zyll de Jong (1983). However, a sub-group within this eastern clade, consisting of the specimens from Gogama, Ontario, and Sept-Îsles, Quebec, are identified by both Diersing (1980) and van Zyll de Jong (1983) as occurring in the range of *S. h. hoyi*. Diersing apparently grouped the Pygmy Shrews from these geographical locales as *S. h. hoyi*, based on a plot of the first two principal component axes derived from his morphological analysis of 21 cranial characters (see Diersing 1980, Figure 5). These two geographical regions (i.e., #16-Central Ontario, and #17-Quebec, north of the St. Lawrence) are outliers in the *S. h. hoyi* polygon. If the *S. h. thompsoni* polygon were extended along the first principal component axis (PC 1), it would encompass these populations from Central Ontario and Quebec (and also parts of northern Wisconsin and Michigan, geographical region #13) without overlapping any of the more westerly populations attributed to the subspecies *S. h. hoyi.*

If shrews from these three regions (i.e., #13, #16, and #17) were included within *S. h. thompsoni*, it would lead to a fundamentally different interpretation of the morphological variation between these two taxa. Both Diersing (1980) and van Zyll de Jong (1976) dismissed the taxonomic importance of the observed morphological variance between *S. thompsoni* and *S. hoyi* as being primarily due to a difference in overall size. While this would still be an important factor differentiating some populations of these two taxa, under the alternative clustering arrangement proposed above, they would also be largely differentiated along the second principle component axis (PC 2), suggesting that these two taxa may differ in the "shape" of some dental features. As Diersing (1980) pointed out, populations with high scores on PC 2 have relatively large third unicuspids but relatively narrow distances between unicuspids toothrows. Similar correlations between patterns of morphological differentiation and genetic divergence have been noted in ermine (Fleming and Cook 2002) and in other shrews (Stewart et al. 2002). In summary then, there may be subtle but important morphological differences between "*S. hoyi*" and "*S. thompsoni*".

Speciation in shrews

Various studies of phylogenetic relationships of shrews have demonstrated that a combined morphological and molecular approach is essential for understanding the taxonomy and process of speciation in this group of mammals (Fumagalli et al. 1999; Demboski and Cook 2002; Stewart et al. 2002). These and other studies also make it apparent that soricid species with broad geographic distributions are unlikely to be genetically homogeneous, particularly for mitochondrial DNA encoded molecular markers. An intraspecific analysis of molecular variance in mtDNA control region sequences for 16 populations of Masked Shrews (*S. cinereus*) from across Canada (Stewart and Baker 1997) indicated very strong population substructuring (and, incidentally, little support for traditionally recognized subspecies). This is consistent with rapid rates of molecular evolution (e.g., Martin and Palumbi 1993) and minimal dispersal abilities in such small-bodied mammals.

Pygmy Shrews also have an extensive range in North America, but are slightly smaller (3-4 g) and considerably less common than *S. cinereus* (van Zyll de Jong 1983). Consequently, gene flow across the range of Pygmy Shrews is likely much lower than it would be for Masked Shrews across an equivalent area. The population demographics of Pygmy Shrews should therefore promote rapid speciation given that the homogenizing effects of gene flow are likely minimized. Indeed, the extremely small effective population sizes that are likely to characterize Pygmy Shrews would promote rapid establishment of reciprocally monophyletic groups. The large range of Pygmy Shrews will ensure that various populations occupy different ecological niches (with correspondingly different selective pressures). In summary, then, no matter how you define species (e.g., by the biological, phylogenetic or ecological species concepts), Pygmy Shrews across North America likely represent separate species (that diverged ~0.4-1.7 Myr ago), or at the very least, incipient species. Sample sizes for this study were very small and additional samples from across the range of this species complex need to be examined. Sampling efforts should be particularly concentrated in potential hybrid zones (e.g., Manitoba, northwestern Ontario) in an effort to detect genetic introgression. In addition, the isolated forms, *S. h. winnemana* and *S. h. montanus*, should be analyzed to determine if they are distinct lineages.

Acknowledgments

We would like to thank the following people who helped collect the Pygmy Shrew samples analysed herein: Allan Baker, Mark Engstrom, Sandeep Hindocha, Bob Murphy, Herbert Russell, and Taye Teferi. Funding for this work was provided by an NSERC operating grant (217175) to DTS. MM is supported by an NSERC postgraduate scholarship. We thank Anne Dalziel, Stephen Petersen, and Derek Potter for assistance in the lab. David Nagorsen provided helpful comments on an earlier version of this manuscript.

Literature Cited

Banfield, A. W. F. 1974. The Mammals of Canada. University of Toronto Press, Toronto, Ontario.

Demboski, J. R., and **J. A. Cook.** 2001. Phylogeography of the dusky shrew, *Sorex monticolus* (Insectivora, Soricidae): insight into deep and shallow history in northwestern North America. Molecular Ecology 10: 1227–1240.

Diersing, V. E. 1980. Systematics and evolution of the pygmy shrews (subgenus *Microsorex*) of North America. Journal of Mammalogy 61: 76–101.

Fleming, M. A., and **J. A. Cook.** 2002. Phylogeography of endemic ermine (*Mustela erminea*) in southeast Alaska. Molecular Ecology 11: 795–807.

Fumagalli, L., P. Taberlet, D. T. Stewart, L. Gielly, J. Hausser, and **P. Vogel.** 1999. Molecular phylogeny and evolution of *Sorex* shrews (Soricidae: Insectivora) inferred from mitochondrial DNA sequence data. Molecular Phylogenetics and Evolution 11: 222–235.

George, S. B. 1988. Systematics, historical biogeography, and evolution of the genus *Sorex*. Journal of Mammalogy 69: 443–461.

Hall, E. R., and **K. R. Kelson.** 1959. The mammals of North America. Volume 1. The Ronald Press Company, New York.

Hutterer, R. 1993. Order Insectivora. Pages 69-130 *in* Mammal Species of the World: a Taxonomic and Geographic Reference, 2nd edition. *Edited by* D. E. Wilson and D. M. Reeder. Smithsonian Institution Press, Washington, D.C.

Irwin, D. M., T. D. Kocher, and **A. C. Wilson.** 1991. Evolution of the cytochrome *b* gene of mammals. Journal of Molecular Evolution 32: 128–144.

Kumar, S., K. Tamura, I. B. Jakobsen, and **M. Nei.** 2001. MEGA2: Molecular Evolutionary Genetics Analysis software. Bioinformatics 17: 1244–1245

Long, C. A. 1972. Taxonomic revision of the mammalian genus *Microsorex* Coues. Transactions of the Kansas Academy of Science. 74: 181–196.

Long, C. A. 1974. *Microsorex hoyi* and *Microsorex thompsoni*. Mammalian Species 33: 1–4.

Martin, A. P., and **S. R. Palumbi**. 1993. Body size, metabolic rate, generation time, and the molecular clock. Proceedings of the National Academy of Science, USA. 91: 4087–4091.

Palumbi, S. J. 1996. PCR and molecular systematics. Pages 205-247 *in* Molecular Systematics, 2nd edition. *Edited by* D. Hillis, C. Moritz, and B. Mable. Sinauer Associates, Sunderland, MA.

Stewart, D. T., and **A. J. Baker.** 1994. Evolution of mtDNA D-loop sequences and their use in phylogenetic studies of shrews in the subgenus *Otisorex* (*Sorex*: Soricidae: Insectivora). Molecular Phylogenetics and Evolution 3: 38–46.

Stewart, D. T., and **A. J. Baker.** 1997. A phylogeny of some taxa of masked shrews (*Sorex cinereus*) based on mitochondrial DNA D-loop sequences. Journal of Mammalogy 78: 361–376.

Stewart, D. T., N. Perry, and **L. Fumagalli.** 2002. The maritime shrew, *Sorex maritimensis* (Soricidae: Insectivora): a newly recognized, Canadian endemic. Canadian Journal of Zoology 80: 94–99.

Swofford, D. L. 2000. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4. Sinauer Associates, Sunderland, Massachusetts.

Thompson J. D., D. G. Higgins, and **T. J. Gibson.** 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Research 22: 4673–4680.

Van Zyll de Jong, C. G. 1976. Are there two species of Pygmy Shrews (*Microsorex*)? Canadian Field-Naturalist 90: 485–487.

van Zyll de Jong, C. G. 1983. Handbook of Canadian Mammals. Volume 1. Marsupials and Insectivores. National Museums of Canada, Ottawa.

Received 4 October 2001
Accepted 13 June 2003

Reintroducing Fire for Conservation of Fescue Prairie Association Remnants in the Northern Great Plains

J. T. Romo

Department of Plant Sciences, University of Saskatchewan, 51 Campus Drive, Saskatoon, Saskatchewan S7N 5A8 Canada

Romo, J. T. 2003. Reintroducing fire for conservation of Fescue Prairie Association remnants in the Northern Great Plains. Canadian Field-Naturalist 117(1):89–99.

The wide geographic distribution, variable climates and associated vegetation, different species of rough fescue, and presumed area-specific fire histories give rise to a range of plant community responses of the Fescue Prairie Association to burning. These variable responses represent potential opportunities for using fire to conserve the biodiversity of Fescue Prairie. Fire can be reintroduced as a process to create temporal and spatial variation in composition, structure, and functioning in a mosaic. This variability can be achieved by reintroducing fire throughout the year, altering the frequency and the proportion of prairie remnants burned, and by using many types of fires. In most cases specific burning prescriptions are not needed to reintroduce fire as a process that is essential for maintaining structure, functioning and composition in Fescue Prairie remnants. A primary goal for conserving Fescue Prairie remnants should be to reintroduce fire as a process to create and maintain patterns and diversity in species assemblages and species composition.

Key Words: Ecosystem management, *Festuca campestris, Festuca hallii,* fire history, natural variability, prairie remnants, restoration, rough fescue, Montana, Alberta, Saskatchewan.

Fire is a natural process in the Fescue Prairie Association (hereafter also referred to as Fescue Prairie, Fescue or Fescue community), but its rhythms and patterns have been altered from the prehistoric period. The purpose of this discussion is to illustrate the variable effects of burning on Fescue-dominated grassland in the Northern Great Plains, and consider how burning may be reintroduced into remnants of Fescue Prairie to approximate the fires that once occurred as a natural process in this ecosystem. Responses to fire in Plains Rough Fescue (*Festuca hallii* (Vasey) Piper) and Mountain Rough Fescue (*F. campestris* Rydb.) and the communities they dominate will be covered, leading to an analysis of the extent to which fire is necessary to maintain structure, functioning and composition in the Fescue Prairie Association. The idea of conserving remnants of Fescue Prairie as a shifting mosaic of different size burns in various stages of recovery after burning and each with unique histories of disturbance, rather than managing for specific species composition, will form the thrust of this discussion. In presenting these ideas, there is no intent to imply forgoing safety issues. Safety should always be a primary concern when using fire as a process for conservation of natural areas.

The Fescue Prairie Association

The Fescue Prairie Association is widespread in western North America. This association is most extensive and has been described in Saskatchewan (Coupland and Brayshaw 1953; Coupland 1961, 1992; Looman 1969; Baines 1973; Cameron 1975*), Alberta (Moss 1944; Moss and Campbell 1947; Looman 1969; Stringer 1973; Rowe and Coupland 1983), Interior British Columbia (Tisdale 1947; McLean and Marchand 1968; Looman 1969) and Montana (Stickney 1960; Ross and Hunter 1976; Mueggler and Stewart 1980). The most extensive and continuous stands of Fescue Prairie on the Northern Great Plains are present in Montana, Alberta, and Saskatchewan (Figure 1). The ecology of Fescue Prairie in southeastern Saskatchewan and southwestern Manitoba is poorly understood because most of the land in this area was cultivated before ecologists could describe and determine the extent of this grassland (R.T. Coupland, personal communication).

Isolated stands of Mountain and Plains rough fescue extend beyond the normal range (*sensu* Coupland 1961; Gould and Shaw 1983) of the Fescue Association. This association is present well into the drier Mixed Prairie on northerly aspects and at higher elevations in southern Saskatchewan and Alberta, and on island-like mountains such as the Cypress Hills in southern Alberta and Saskatchewan, and the Sweetgrass Hills and Bears Paw Mountains in northern Montana. Small outlier Fescue Prairies have been described in Riding Mountain National Park in Manitoba (Blood 1966; Looman 1969; Trottier 1986), northwestern North Dakota (Cosby 1965), and northeastern Washington (Hodgkinson and Young 1973).

Fescue Prairie lies in an environment that is conducive to tree growth, and is maintained by periodic drought and fire (R.T. Coupland, personal communication). Annual temperatures average about 4°C or less (Coupland and Brayshaw 1953) where Fescue dominates, and most precipitation is received in May through July (Figure 2). The least precipitation is received from about October through March or

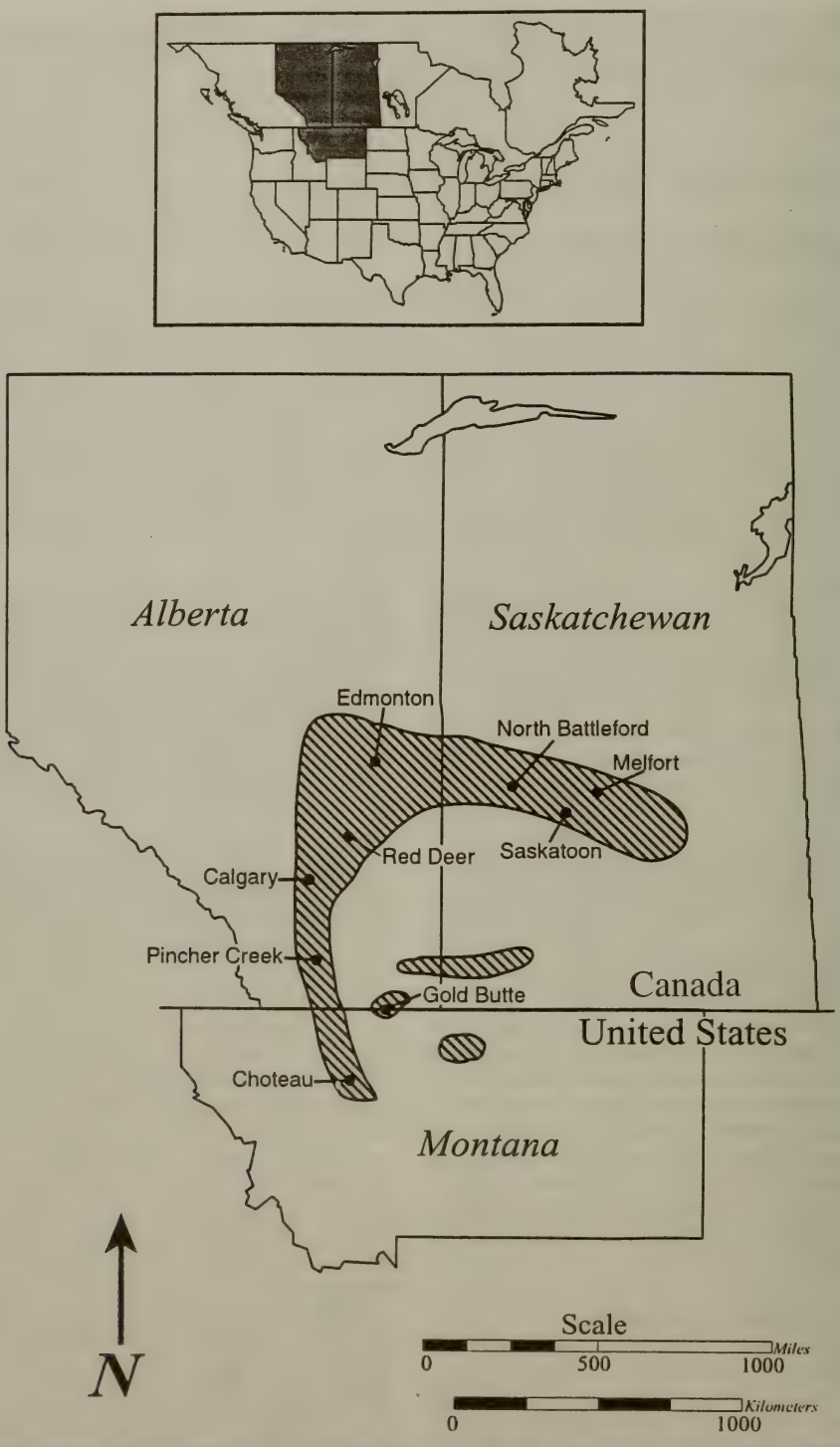


FIGURE 1. Cross-hatched patterns indicate the general distribution of the Fescue Prairie Association in the Northern Great Plains. The names indicate weather stations for which weather data were examined.

April. The Fescue Association intermingles with forests of Lodgepole Pine (*Pinus contorta* Dougl.), Ponderosa Pine (*P. ponderosa* Dougl.), Douglas Fir (*Pseudotsuga menziesii* (Mirbel) Franco) (Pfister et al. 1977; Arno and Gruell 1986), Limber Pine (*Pinus flexilis* James) (Barrett 1999*), Jack Pine (*Pinus banksiana* Lamb.) and Trembling Aspen (*Populus tremuloides* Michx.) (Cameron 1975*; Trottier 1985). Trees and shrubs encroach upon Fescue Prairie in the absence of burning, eventually gaining dominance in the plant community (Johnston and Smoliak 1968; Bailey and Wroe 1974; Bailey 1978; Bailey and Anderson 1978; Anderson and Bailey 1980; Archibold and Wilson 1980; Arno and Gruell 1986). Rates of tree and shrub encroachment have been estimated at about 0.75% per year (Johnston and Smoliak 1968; Bailey 1978).

The Fescue Association is not dominated by a single species of *Festuca* in the Northern Great Plains (see Harms 1985). Plains Rough Fescue (*Festuca hallii* (Vasey) Piper), a weakly rhizomatous perennial, dominates on the Northern Great Plains *per se* while the tussock-forming, Mountain Rough Fescue (*F. campestris* Rydb.) tends to prevail in the foothills and mountains on the western edge of the Northern Great Plains. As might be expected the boundaries between areas where Plains and Mountain rough fescue dominate this association are not clear, nor are they documented. Up to about 200 species of vascular plants grow in Fescue Prairies (Moss and Campbell 1947; Coupland and Brayshaw 1953; Anderson and Bailey 1980; Antos et al. 1983; Pylypec 1986; Bork et al. 2002). Less than 5% of the grassland dominated by Plains Rough Fescue remains in Saskatchewan, primarily as small and isolated remnants (Grilz and Romo 1995), and this once extensive prairie is one of the most threatened ecosystems on the Canadian Prairies (World Wildlife Fund 1988). About 15% of the Fescue Prairie remains in its native state in Alberta (Alberta Prairie Conservation Forum 2001*).

Response of Fescue and Fescue-Dominated Communities to Fire

Depending on the season of burning and the fire return interval, Plains Rough Fescue increases (Bailey and Anderson 1978; Trottier 1985*; Driver 1987*), decreases (Bailey and Anderson 1978; Anderson and Bailey 1980) or does not change (Trottier 1985*). Reductions in Plains Rough Fescue can last up to three years after burning (Bailey and Anderson 1978). Herbage production by Plains Rough Fescue is unaffected after spring or fall burning (Bailey and Anderson 1978), or reduced up to three years, with greater reductions following fall as compared to spring burning (Redmann et al. 1993). Delaying burning in the spring reduces yield apparently because fire damages growing plants (Gerling et al. 1995).

Fall or spring burning of Plains Rough Fescue in Saskatchewan did not alter tiller densities (Grilz and Romo 1995), but tillering was stimulated by the spring burning in central Alberta (Gerling et al. 1995). Inflorescence production of Plains Rough Fescue is reduced (Toynbee 1989) or unaffected by burning in the fall (Bailey and Anderson 1978), or reduced after spring burning (Anderson and Bailey 1980; Toynbee 1989) with greatest reductions caused by late spring burning (Toynbee 1989). Burning in April or June can stimulate inflorescence production whereas July or October fires have no effect (Gerling et al. 1995).

Not unexpectedly, burning alters the composition of Plains Rough Fescue-dominated communities and reflects stress of individual species at the community level (Stueter and McPherson 1995). Species richness is reduced (Bailey and Anderson 1978; Grilz and Romo 1995), enhanced (Anderson and Bailey 1980; Grilz and Romo 1995) or unaffected (Driver 1987*) by fall or spring burning. Repeated, annual burning of Fescue Prairie in the Aspen Parkland can change the plant community from one dominated by shrubs and/or Plains Rough Fescue to another characterized by species of the more arid Mixed Prairie (Bailey 1978; Anderson and Bailey 1980; Driver 1987*). Forbs (Bailey and Anderson 1978; Trottier 1985*) and shrubs (Bailey and Anderson 1978) tend to increase after fall or spring burning with equivocal responses in the two seasons (Trottier 1985*). By comparison native graminoids increased following spring or fall burning on prairie dominated by Plains Rough Fescue, but forbs were unaffected (Grilz and Romo 1995). Different species of grasses, sedges and rushes, forbs, and shrubs can be categorized as increasers, decreasers, or as being unaffected by burning (Anderson and Bailey 1980).

Less is known about the response of Mountain Rough Fescue to burning. Burning reduces cover of the grass (Antos et al. 1983; Bork et al. 2002) and productivity can decline (Jourdannais and Bedunah 1990). Spring or fall burning as well as head and back fires had no effect on the density of Mountain Rough Fescue in the foothills of the Rocky Mountains in north-central Montana (Jourdannais and Bedunah 1990). Recovery of plant cover and herbage production in the second growing season after a December wildfire in the foothills of southwest Alberta was attributed to higher than normal growing season precipitation after burning (Bork et al. 2002). Bork et al. (2002) further concluded that it would take several years for litter to recover after burning.

Burning Mountain Rough Fescue communities in the Rocky Mountain foothills in Montana had no effect on shrubs and forbs, but perennial grasses were reduced for two years (Jourdannais and Bedunah 1990). Species richness and total plant

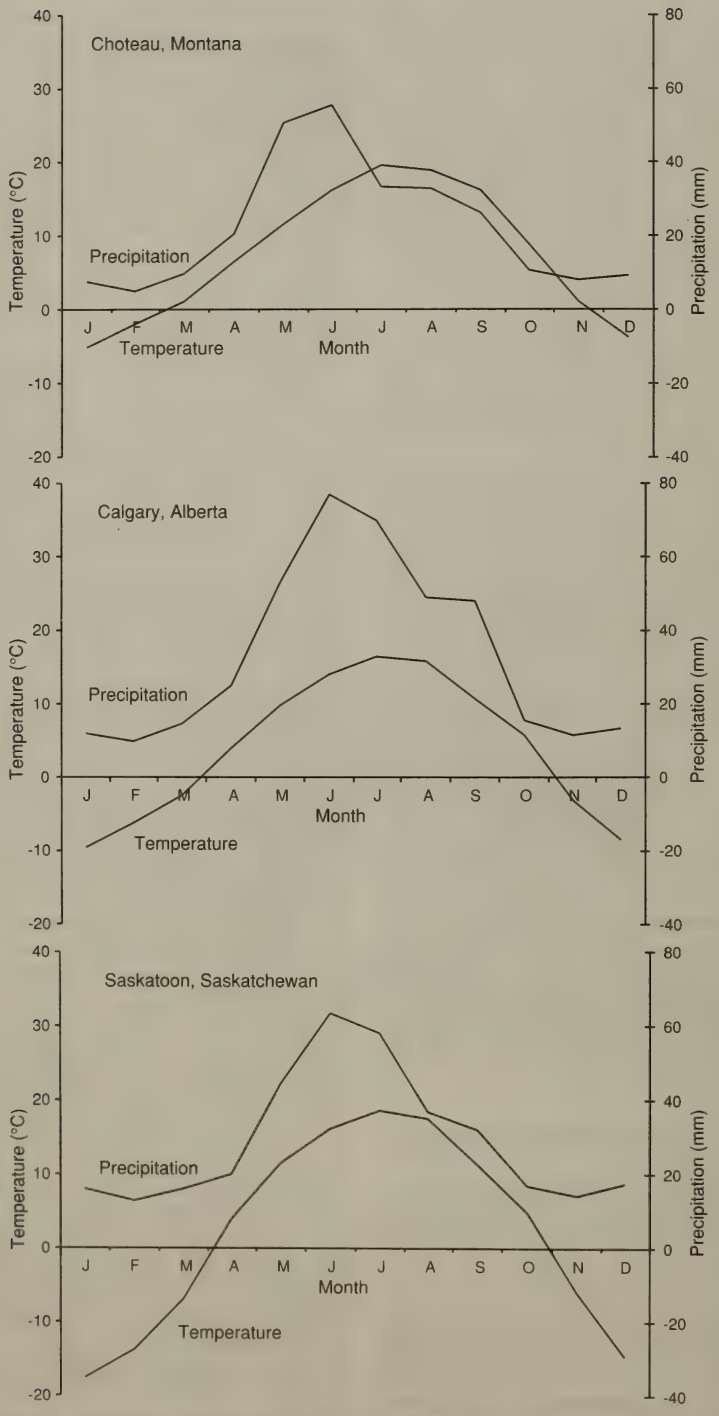


FIGURE 2. Plots of precipitation and temperature for three weather stations in or near the Fescue Prairie Association in Montana, Alberta, and Saskatchewan. Weather data for Choteau, Montana were provided upon special request by the United States National Oceanic and Atmospheric Administration, Western Region Office, Reno, Nevada, and for Calgary, Alberta and Saskatoon, Saskatchewan by Environment Canada, Saskatoon Office, Saskatoon, Saskatchewan.

cover did not change after early summer burning, but forbs increased while perennial grasses decreased; bryophytes and lichens were severely reduced (Antos et al. 1983). Mirophytic cover was unaffected by burning in the winter in Alberta (Bork et al. 2002). Compared to unburned areas, diversity and richness of vascular plants were unaffected by a wildfire in December (Bork et al. 2002).

Although a host of environmental factors are altered by burning in grasslands (see Daubenmire 1968; Wright and Bailey 1982), changes in the composition of Mountain and Plains rough fescue-dominated communities have also been attributed to an altered microenvironment, particularly moisture regimes. Reduced soil water and increased water stress in plants (Redmann 1978; Antos et al. 1983; Redmann et al. 1993; Romo et al. 1993; Grilz and Romo 1994) is caused by limited snow trapping (Redmann et al. 1993; Romo et al. 1993), decreased infiltration and increased evaporation (DeJong and MacDonald 1975). After burning, plants may also be exposed to lower (Romo et al. 1993) or higher ambient temperatures and greater diurnal fluctuations (Antos et al. 1983), slowing growth. Environmental conditions may outweigh burning impacts, especially in years of low precipitation (Grilz and Romo 1994), and favorable climatic conditions speed recovery of the community (Jourdannais and Bedunah 1990; Redmann et al. 1993; Pylypec and Romo 2002; Bork et al. 2002). Direct damage to plants from burning, especially when plants are growing, has also been implicated in changing species composition in Fescue Prairie (Bailey and Anderson 1978).

Timing of Fires in Fescue Prairie

Historical records indicate fires occurred every month of the year in the Northern Great Plains (Higgins 1986), and consecutive decades had high and low fire occurrences (Umbanhowar 1996). Bailey (1978, 1986) reported that Fescue Prairie might be burned with one to three days of drying after the melting of snow or after precipitation events. Our own experience in central Saskatchewan has shown that Fescue Prairie will burn within one day of drying.

Examination of weather records for two weather stations in Montana, four stations in Alberta, and three in Saskatchewan revealed that the probability of conditions being suitable for burning during the winter (November though March) vary considerably in the Fescue Prairie. The likelihood of ≥3 consecutive snow-free days per month is generally least during January and February (Table 1). In the foothills of the Rocky Mountains the probability of ≥3 consecutive snow-free days each winter month ranges from about 60 to 100% (Table 1) because the warm, dry winds of Chinooks frequently descend the eastern slopes of the Rocky Mountains and melt snow. At distances further north and east of the Rocky Mountains such as Red Deer and Edmonton, Alberta and Saskatchewan (Figure 1), the snow-melting effect of Chinooks diminishes, snow cover is more persistent, and the chance of ≥3 consecutive days snow-free days is considerably less.

That the probability of conditions being conducive to burning during the winter is high in Fescue Prairie along the foothill of the Rocky Mountains is corroborated by Peter Fidler's accounts while traveling in southwest Alberta in 1792–1793 (Fidler 1991). Fidler reported "...Every fall and spring and even in the winter when there is no snow, these large plains either in one place or other is constantly on fire.... The lightning in the spring and fall frequently light the grass and in the winter it is done by Indians". In another account in 1858 near Pigeon Lake, southwest of Edmonton, Alberta, John Palliser (Palliser 1968) wrote "...The morning was very bright, and although the thermometer stood at 11°,...we set fire

TABLE 1. The probability of at least three consecutive snow-free days from November through March in Fescue Prairie on the Northern Great Plains in Montana, Alberta, and Saskatchewan. Weather data were provided by the United States National Oceanic and Atmospheric Administration, Western Region Office, Reno, Nevada, and Environment Canada, Saskatoon, Saskatchewan office upon special request.

Month	Montana		Alberta				Saskatchewan		
	Choteau	Gold Butte	Pincher Creek	Calgary	Red Deer	Edmonton	North Battleford	Saskatoon	Melfort
	(%)								
November	100	100	100	97	92	87	86	89	93
December	87	100	87	74	32	34	33	26	23
January	88	95	75	61	8	3	3	5	0
February	89	100	92	66	11	3	0	8	0
March	100	100	96	97	32	58	29	53	20
Mean	93	99	90	79	35	37	30	36	27

to the grass, just to say we had done so, on the 10th of January." These accounts suggest that both human- and lightning-caused fires should be considered part of the historic fire regime. Historically aboriginal- and lightning-caused fires would have created a mosaic of burnt patches with different times of ignition, sizes, shapes and configuration in the Fescue Prairie.

Periods of low precipitation in spring and early summer (April through May) and late summer through fall (late July through October) most consistently present conditions for burning in Fescue Prairie. Let there be no doubt that Fescue Prairie is extremely flammable before late spring and early summer rains materialize and plants grow, and after plants have matured in late summer and fall before snow is received. Raby (1966), Russel (1971), and Higgins (1986) all cited numerous accounts of fires occurring during these times. Even today, wildfires occur during these periods and prescribed burns are often conducted then.

Further examination of precipitation records revealed a 100% probability of ≥3 consecutive days of drying conditions in the Fescue Prairie from April through October. The amount of accumulated, fine, dead plant material and its moisture content will play major roles in determining whether Fescue Prairie will burn during this period. In an ongoing study of burning in an ungrazed, Plains Rough Fescue-dominated prairie at Saskatoon, Saskatchewan, we have conducted burns during all months of the year except January and February. In addition, we have burned on this prairie in all summer months, even in years when summer precipitation was above normal.

Fire Return Intervals

Several fire return intervals have been proposed for Fescue Prairie. Short- or long-return intervals between fires are detrimental to Mountain Rough Fescue, and frequencies of five to ten years may minimize damage to individual plants and have limited effects on species composition (Antos et al. 1983). Five- (Trottier 1985*) to ten- (Wright and Bailey 1982) year return intervals limit invasion of Fescue Prairie by trees or shrubs. Nitrogen losses in fires exceed annual deposition of this nutrient in Plains Rough Fescue communities, prompting Redmann (1991) to conclude that burning more frequently than every four years may upset the nitrogen balance of the ecosystem. Reduced amounts of litter are a persistent effect of burning on Mountain (Jourdannais and Bedunah 1990; Bork et al. 2002) and Plains rough fescue communities (Redmann et al. 1993; Pylypec and Romo in press), and although a time was not specified, several years are required for its recovery. Pylypec and Romo (in press) studied recovery of litter and total standing crop, and suggested that fire return intervals of at least ten to 11 years should be considered in Fescue Prairie.

Using fire-scarred trees, Barrett (1997*) estimated fire return intervals for the period between 1726 and 1936 averaged about ten years and ranged from one to 40 years in forests adjacent to Fescue Prairie in the foothills of the Rocky Mountains near Glacier National Park, Montana. Dating back to 1658, the fire interval ranged from five to 28 years, and averaged 12 years near Choteau, Montana, while the average return interval of fires was 26 years, and ranged from 10 to 60 years on the Crown Butte Preserve near Simms, Montana (Barrett 1999*). Despite the lack of consensus regarding fire return intervals, these observations illustrate that considerable variation in fire return intervals was characteristic of the Fescue Prairie Association and should be considered when re-introducing fire. Evidence also suggests, however, that the fire return interval has been lengthened (Barrett 1997*, 1999*) either because of purposeful fire suppression or landscape modification.

Spatial Relations of Fires

Historically, burns on the Northern Great Plains were relatively small (Higgins 1984). Burns in Fescue Prairie were likely smaller in the foothills of the Rocky Mountains than on the plains because landscape irregularities create natural firebreaks (A.W. Bailey, personal communication). Fires were likely patchy in time and space, and even though Fescue Prairie developed with fire at the landscape level, this process no longer functions at that scale because of extensive modification of the landscape by humans. This landscape modification was recognized as early as 1898 when the Royal Canadian Mounted Police (RCMP) superintendent at Fort Saskatchewan, Alberta reported "...fires do not run...(as) they used to, and the new roads being ploughed up and made have a great influence in checking the spread of these fires..." (Raby 1966). Another account from the RCMP at Prince Albert, Saskatchewan stated "...the extent of the area burned over is not so large. This is doubtless due to the fact that whereas large tracts of land used to remain unbroken by road or fireguard, the country is subdivided to such an extent that a fire is soon automatically stopped by its coming into contact with a road or similar obstruction." (Raby 1966). Landscape modification has continued to the point that fires are now infrequent or excluded in the small and widely scattered remnants of Fescue Prairie, creating challenges in many conservation issues.

Reintroducing Fire to Fescue Prairie Remnants

Prescriptions for burning Fescue Prairie have been developed by Bailey (1978, 1986) and Trottier (1985*). Bailey's (1978, 1986) prescriptions were developed primarily to control tree and shrub invasion in grassland (A.W. Bailey, personal

communication), while those reported by Trottier (1985) were intended to duplicate historic burns in autumn or spring. These prescriptions are effective in defining safe limits to burning and meeting the intended purposes. However, it may be useful to develop approaches that include more heterogeneity in burning when burning in Fescue Prairie is framed within the concepts of ecosystem management (Bourgeron and Jensen 1994; Jensen and Everett 1994; Kaufmann et al. 1994; Dale et al. 2000), applied historical ecology (Swetnam et al. 1999), natural variability (Landres et al. 1999), landscape ecology (Urban 1994; Dale et al. 2000), and the natural disturbance regime (Hobbs and Huenneke 1992). Burning only in spring and fall under specific prescriptions precludes variation in burns that would have existed under the historic natural fire regime. Disruption of historic fires regimes has changed the diversity of habitats on the Great Plains (Seig et al. 1999), and biodiversity is diminished when fire regimes are altered on prairie landscapes (Leach and Givnish 1996).

Even though fall and spring are popular times to conduct prescribed burns in Fescue Prairie, it is proposed that, for conservation purposes, burning should be considered for any time in which it can be safely conducted. This proposition is based on the fact that although climatic conditions may not be conducive to burning every month of each year, suitable conditions likely occur each month over a span of several years. Sometimes the conditions for burning will be marginal relative to prescriptions (see Bailey 1978, 1986), but these situations will give rise to unique fire behavior and patterns of combustion, leading to increased heterogeneity in the prairie. The importance of variable times of burning in changes in species abundance in Tallgrass Prairie has been reported (Howe 1994 a,b, 1995), and as shown previously, plant community responses to burning also vary widely among burns in Fescue Prairie. Burning throughout the year will undoubtedly lead to fires and responses that are quite different than most people envisage or have become accustomed to, further challenging perspectives of how prairies should be burned. Fires will span the continuum from those of high intensity and uniform combustion to spotty and low intensity ones. Variation in the effects of burning can be added by using different ignition patterns and types of fires (see Wright and Bailey 1982).

Perhaps the most challenging aspect of re-introducing fire in Fescue Prairies is determining the amount of the remnant that should be burned. Fire patterns that occurred at large scales cannot be reintroduced and maintained in prairie remnants that are only a fraction of the original landscape in size. One alternative is to simulate temporal and spatial patterns on a smaller scale realizing there will be shortcomings compared to that which historically occurred at large scales.

As suggested by state-space relationships (see Turner et al. 1993, 1994a,b), the size of the burn as a proportion of the landscape, or in this case the remnant prairie, should be considered in conjunction

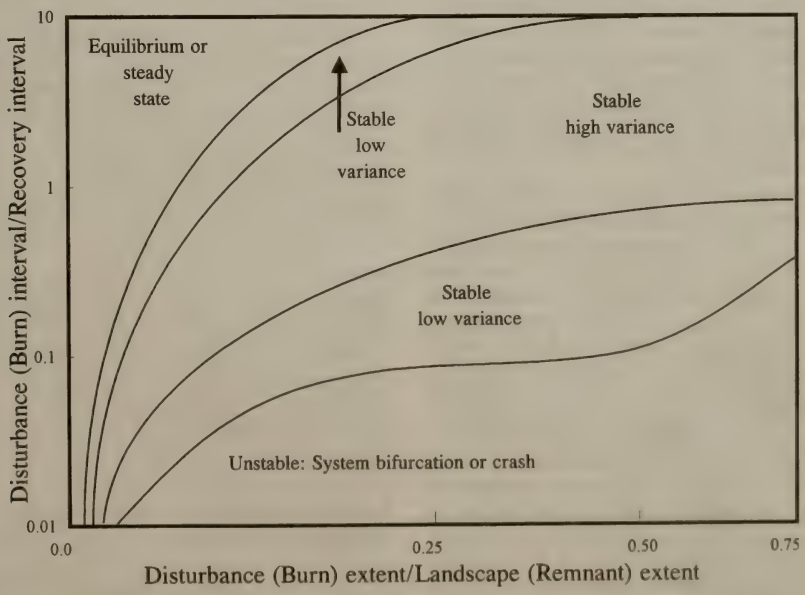


FIGURE 3. A state-space model of temporal and spatial relationships of landscapes in relation to disturbance. Adapted from Turner et al. (1993, 1994a,b).

with states of recovery from previous burns (Figure 3). Recovery interval is the time elapsed from the time of disturbance (burning) until the burned patch is fully recovered from the effects of burning. Thus when the disturbance interval/recovery interval (DI/RI) for a burned patch is ≥1, the structure, composition and functioning has recovered from the previous burn. In contrast a burnt patch in which the structure, functioning, and composition have not completely recovered has a DI/RI <1. This state-space model predicts remnants will be in equilibrium or a steady state if about 25% or less of the remnant is burned, and a wide range in states of recovery from burning are represented in relatively small burn patches. In this situation burnt patches are small and variability in their size is limited, however, and most of the remnant has a DI/RI >1.

This model further predicts that a wide range of fire return intervals and burn sizes in the remnant will maximize temporal and spatial variability among burn patches, and thus the remnant. If a wide range of DI/RI is preserved and the proportion of the remnant that is burned is increased, it is predicted that the remnant will remain stable, and variation within the remnant will be related to variation in the size of burned patches. In other words, maximum variation in the remnant will arise when variation is maximized in both DI/RI and the size of burned patches. By comparison, if most of the remnant is burned frequently and maintained primarily in early stages of recovery (DI/RI ≤1), it is predicted that variation will be limited because the proportion of the remnant in various recovery stages is skewed toward DI/RI ≤1. Frequently burning remnants (DI/RI <1) is predicted to cause significant changes because some species cannot recover or reestablish after frequent and extensive burning. This later prediction appears realistic because annual burning (DI/RI <1) of Fescue Prairie leads to plant communities that are characteristic of Mixed Prairie (Anderson and Bailey 1980).

This state-space model can be used to guide reintroduction of fire as a process in remnants of Fescue Prairie, with the burn interval/recovery time and burn size/remnant size being important considerations. Fire return intervals ranging from 1 to 60 years (Wright and Bailey 1982; Antos et al. 1983; Trottier 1985*; Redmann 1991; Barrett 1997*, 1999*; Pylypec and Romo in press) should be included as should burn patches of various sizes. Presumably this approach will provide habitats for fire-sensitive species and those that respond favorably to burning. Although burning entire prairie remnants may satisfy needs of some organisms requiring large habitats, it may also jeopardize those requiring habitats in various stages of recovery. Since the state-space model is based on proportions, the actual size of the burns will increase with remnant size because burns are scaled to the size of each remnant. Habitat needs of area-sensitive organisms are more likely to be met as remnant size increases.

Implementing Conservation Burning

Conservationists are challenged to find ways of incorporating variability in processes if conservation of biodiversity in natural ecosystems is to be successful. Reintroducing and/or maintaining ecosystem processes are paramount (West 1993) in conservation as is providing diversity of structure and successional stages (Sieg et al. 1999). Specifically, it is necessary to consider how fire should be reintroduced and maintained given that most Fescue Prairie remnants are small and isolated.

Research in Fescue Prairie has clearly illustrated that burning produces extremely variable responses. These wide ranging responses reflect unique species reactions that are tempered by burn, site, and environmental conditions. Presumably different fire histories under which the species and communities developed over time also influence the effects of burning. Variable responses to burning are not restrictions to conservation, but they are integral in maintaining diversity at the genetic, species, community, ecosystem and landscape levels (Christensen 1988). Maintaining particular patterns in Fescue Prairie should not be the preoccupation of conservationists; instead, emphasis should be placed on reintroducing and maintaining ecosystem processes and their rhythms that are responsible for creation of patterns. If the processes involved in the development and maintenance of ecosystems are present, then ecosystems and patterns are more likely to persist than if processes are removed or altered (Hobbs and Huenneke 1992).

Restoring natural rhythms and processes to other ecosystems is also important in the conservation of Fescue Prairie. Fescue Prairie remnants are not isolated entities, and surrounding ecosystems and land management activities must also be considered. Surrounding land uses (Forman 1995) have major impacts on remnant Fescue Prairies (Romo et al. 1990; Grilz and Romo 1994, 1995). Fire must be reintroduced to the surrounding forests and shrub-dominated communities for they invade Fescue Prairie in the absence of burning (Johnston and Smoliak 1968; Bailey and Wroe 1974; Bailey 1978; Anderson and Bailey 1979; Anderson and Bailey 1980; Arno and Gruell 1986; Barrett 1997*, 1999*).

Except in certain instances, rather than focusing on specific issues with special plans, the prescription for burning should simply be to reintroduce fire as a process to regulate structure, functioning and composition in remnants of the Fescue Prairie Association. This approach assumes that all fires and the variation among them are needed for the persistence of biodiversity in this ecosystem, and they should be reintroduced and maintained until shown otherwise. Leach and Givnish (1996) argued that prairie remnants

should include burned and unburned patches so fire sensitive species are not extirpated. A mosaic of habitat patches in various stages of recovery from burning is essential because a variety of arthropod species are killed by burning and must recolonize from unburned habitats (Panzer 1988*; Harper et al. 2000). Maintaining habitats in various successional stages after burning is an important consideration because some prairie bird species respond negatively to burning while others select burned habitats (Renken and Dinsmore 1987; Pylypec 1991; Herkert 1994; Madden et al. 1999, 2000).

Frequencies and sizes of fires are important to consider when reintroducing fire to prairie remnants. Including non-static times and locations of burning, along with a range of burn sizes, fire types, ignition patterns, and return intervals will create heterogeneous fire effects in a shifting mosaic. Each patch will have a unique fire history that will add to the resistance and resilience of the association. Taken together, the remnant will resemble a constantly changing collage in which many layers of images with different composition, size, and shapes are overlying one another.

The structure, composition and functioning of the Fescue Prairie that develops under a fire regime that is based on the historic patterns may not be what is anticipated. The current character of most Fescue Prairie remnants is the result of altered fire regimes. It may be worthwhile for conservationists to reconsider whether it is appropriate to manage for biological diversity or whether conservation activities should include processes that are required to create and maintain biodiversity. Furthermore, conservation of Fescue Prairie remnants should be focused on natural processes, assuming they are important. If variation in burning is presumed unimportant and is not reintroduced and maintained, an essential process in the structuring of the plant communities may be omitted. Efforts can be focused on other aspects of conservation if it is learned that natural processes such as burning are not essential for conservation of Fescue Prairie.

Acknowledgments

I thank Rick Young for engaging in numerous discussions on the conservation of natural ecosystems, and especially the topic of fire ecology. R.E. Redmann, Tyler Colberg and two anonymous reviewers provided useful comments and suggestions for improvement on an earlier draft. An earlier version of this paper was presented at the Parks Canada National Prescribed Fire Workshop, 1-4 October 1996 in La Mauricie National Park, Quebec.

Documents Cited [marked * in text]

Alberta Prairie Conservation Forum. 2001. http://www.albertapcf.ab.ca/. 23 June 2003.

Barrett, S. W. 1997. Fire history of Glacier National Park: Hudson Bay drainage. U.S.D.I. National Park Service Contract CX 1430-5-0001. Final Report. 46 pages.

Barrett, S. W. 1999. Fire regimes on the Pine Butte Swamp Preserve, Montana. Final Report for The Nature Conservancy. 13 pages.

Cameron, T. F. 1975. Fescue grasslands and associated communities of Prince Albert National Park, Saskatchewan. Parks Canada Contract 72-66. 299 pages.

Driver, E. A. 1987. Prescribed burn project: Experimental prescribed burning on the Last Mountain Lake Wildlife Management Unit. Progress Report: Post treatment year 1986. Canadian Wildlife Service, Saskatoon, Saskatchewan. 88 pages.

Trottier, G. C. 1985. Evaluation of the prescribed burn study, Prince Albert National Park. Parks Research Group, Canadian Wildlife Service. Edmonton, Alberta. 139 pages.

Literature Cited

Anderson H. G., and **A. W. Bailey.** 1980. Effects of annual burning on grassland in the aspen parkland of east-central Alberta. Canadian Journal of Botany 58: 985–996.

Anderson, M. L., and **A. W. Bailey.** 1979. Effect of fire on a *Symphoricarpos occidentalis* shrub community in central Alberta. Canadian Journal of Botany 57: 2819–2823.

Antos, J. A., B. McCune, and **C. Bara.** 1983. The effect of fire on an ungrazed western Montana grassland. American Midland Naturalist 110: 354–364.

Archibold, O. W., and **M. R. Wilson.** 1980. The natural vegetation of Saskatchewan prior to agricultural settlement. Canadian Journal of Botany 58: 2031–2042.

Arno, S. F., and **G. E. Gruell.** 1986. Douglas-fir encroachment into mountain grasslands in southwestern Montana. Journal of Range Management 39: 272–276.

Bailey, A. W. 1978. Use of fire to manage grasslands of the Great Plains: Northern Great Plains and adjacent forests. Proceedings of the First International Rangeland Congress 1: 691–693.

Bailey, A. W. 1986. Prescribed burning for range and wildlife management. Agriculture and Forestry Bulletin 9: 10–14.

Bailey, A. W., and **M. L. Anderson.** 1978. Prescribed burning of a *Festuca-Stipa* grassland. Journal of Range Management 31: 446–449.

Bailey, A. W., and **R. A. Wroe.** 1974. Aspen invasion in a portion of the Alberta parklands. Journal of Range Management 27: 263–266.

Baines, G. B. K. 1973. Plant distributions on a Saskatchewan prairie. Vegetatio 28: 99–123.

Blood, D. A. 1966. The *Festuca scabrella* association of Riding Mountain National Park, Manitoba. Canadian Field-Naturalist 80: 24–32.

Bork, E. W., B. W. Adams, and **W. D. Willms.** 2002. Resilience of foothills rough fescue, *Festuca campestris*, rangeland to wildfire. Canadian Field-Naturalist 116: 51–59.

Bourgeron, P. S., and **M. E. Jensen.** 1994. An overview of ecological principles for ecosystem management. Pages 45–57 *in* Volume II: Ecosystem management: Principles and applications. U.S.D.A. Forest Service

General Technical Report PNW-GTR-318. Portland, Oregon. 376 pages.

Christensen, N. L. 1988. Succession and natural disturbance: Paradigms, problems, and preservation of natural ecosystems. Pages 62–86 *in* Ecosystem management for parks and wilderness. *Edited by* J. K. Agee and D. R. Johnson. University of Washington Press, Seattle.

Cosby, H. E. 1965. Fescue grassland in North Dakota. Journal of Range Management 18: 284–285.

Coupland, R. T. 1961. A reconsideration of grassland classification in the Northern Great Plains of North America. Journal of Ecology 49: 135–167.

Coupland, R. T. 1992. Fescue prairie. Pages 291–295 *in* Natural grasslands: Ecosystems of the world 8A. *Edited by* R. T. Coupland. Elsiever, New York.

Coupland, R. T., and **T.C. Brayshaw.** 1953. The fescue grassland in Saskatchewan. Ecology 34: 386–405.

Dale, V. H., S. Brown, R. A. Haeuber, N. T. Hobbs, N. Huntly, R. J. Naiman, W. E. Riebsame, M. G. Turner, and **T. J. Valone.** 2000. Ecological principles and guidelines for managing the use of land. Ecological Applications 10: 639–670.

Daubenmire, R. 1968. Ecology of fire in grasslands. Advances in Ecological Research 5: 209–266.

DeJong, E., and **K. B. MacDonald.** 1975. The soil moisture regime under native grassland. Geoderma 14: 207–221.

Fidler, P. 1991. Journal of a journey over land from Buckingham House to the Rocky Mountains in 1792 & 93. *Edited by* B. Haig. Historical Research Centre, Lethbridge, Alberta. 100 pages.

Forman, R. T. T. 1995. Land mosaics: The ecology of landscapes and regions. Cambridge University Press, New York. 632 pages.

Gerling, H. S., A. W. Bailey, and **W. D. Willms.** 1995. The effects of burning on *Festuca hallii* in the parklands of central Alberta. Canadian Journal of Botany 73: 937–942.

Gould, F. W., and **R. B. Shaw**. 1983. Grass systematics, 2nd edition. Texas A&M University Press. College Station, Texas. 397 pages.

Grilz, P. L., and **J. T. Romo.** 1994. Water relations and growth of *Bromus inermis* Leyss. (smooth brome) following spring or autumn burning in a fescue prairie. American Midland Naturalist 132: 340–348.

Grilz, P. L., and **J. T. Romo.** 1995. Management considerations for controlling smooth brome in fescue prairie. Natural Areas Journal 15: 148–156.

Harms, V. L. 1985. A reconsideration of the nomenclature and taxonomy of the *Festuca altaica* complex (Poaceae) in North America. Madrono 32: 1–10.

Harper, M. G., C. H. Dietrich, R. L. Larimore, and **P. A. Tessene.** 2000. Effects of prescribed fire on prairie arthropods: An enclosure study. Natural Areas Journal 20: 325–335.

Herkert, J. R. 1994. Breeding bird communities of midwestern prairie fragments: The effects of prescribed burning and habitat-area. Natural Areas Journal 14: 128–135.

Higgins, K. F. 1984. Lightning fires in North Dakota grasslands and pine savanna lands of South Dakota and Montana. Journal of Range Management 37: 100–103.

Higgins, K. F. 1986. Interpretation and compendium of historical fire accounts in the Northern Great Plains. U.S.D.I. Fish and Wildlife Service Resource Publication 161. 39 pages.

Hobbs, R. J., and **L. F. Huenneke.** 1992. Disturbance, diversity, and invasion: Implications for conservation. Conservation Biology 6: 324–337.

Hodgkinson, H. S., and **A. E. Young.** 1973. Rough fescue (*Festuca scabrella* Torr.) in Washington. Journal of Range Management 26: 25–26.

Howe, H. F. 1994a. Managing species diversity in tallgrass prairie: Assumptions and implications. Conservation Biology 8: 691–704.

Howe, H. F. 1994b. Response of early- and late-flowering plants to fire season in experimental prairies. Ecological Applications 4: 121–133.

Howe, H. F. 1995. Succession and fire season in experimental prairie plantings. Ecology 76: 1917–1925.

Jensen, M. E., and **R. Everett.** 1994. An overview of ecosystem management principles. Pages 6–15 *in* Volume II: Ecosystem management: Principles and applications. U.S.D.A. Forest Service General Technical Report PNW-GTR-318. Portland, Oregon. 376 pages.

Johnston, A., and **S. Smoliak.** 1968. Reclaiming brushland in southwestern Alberta. Journal of Range Management 21: 404–406.

Jourdonnais, C. S., and **D. J. Bedunah.** 1990. Prescribed fire and cattle grazing on an elk winter range in Montana. Wildlife Society Bulletin 18: 232–240.

Kaufmann, M. R., R. T. Graham, D. A. Boyce, Jr., W. H. Moir, L. Perry, R. T. Reynolds, R. L. Bassett, P. Mehlhop, C. B. Edminster, W. M. Block, and **P. S. Corn.** 1994. An ecological basis for ecosystem management. U.S.D.A. Forest Service General Technical Report RM-GTR-246. Fort Collins, Colorado. 22 pages.

Landres, P. B., P. Morgan, and **F. J. Swanson.** 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9: 1179–1188.

Leach, M. K., and **T. J. Givnish.** 1996. Ecological determinants of species loss in remnant prairies. Science 273: 1555–1558.

Looman, J. 1969. The fescue grasslands of western Canada. Vegetatio 19: 128–145.

Madden, E. M., A. J. Hansen, and **R. K. Murphy.** 1999. Influence of prescribed fire history on habitat and abundance of passerine birds in northern mixed-grass prairie. Canadian Field-Naturalist 113: 627–640.

Madden, E. M., R. K. Murphy, A. J. Hansen, and **L. Murray.** 2000. Models for guiding management of prairie bird habitat in northwestern North Dakota. American Midland Naturalist 144: 377–392.

McLean, A., and **L. Marchand.** 1968. Grassland ranges in the southern interior of British Columbia. Canada Department of Agriculture Publication 1319. 28 pages.

Moss, E. H. 1944. The prairie and associated vegetation of southwestern Alberta. Canadian Journal of Research (C) 22: 11–31.

Moss, E. H., and **J. A. Campbell**. 1947. The fescue grassland of Alberta. Canadian Journal of Research (C) 25:209-227.

Mueggler, W. F., and **W. L. Stewart.** 1980. Grassland and shrubland habitat types of western Montana. U.S.D.A. Forest Service General Technical Report INT-66. Ogden, Utah. 137 pages.

Palliser, J. 1968. The papers of the Palliser Expedition 1857-1860. *Edited* by I. M. Spry. The Champlain Society, Toronto. 694 pages.

Panzer, R. 1988. Managing prairie remnants for insect conservation. Natural Areas Journal 8: 83–90.

Pfister, R. D., B. L. Kovalchik, S. F. Arno, and **R. C. Presby.** 1977. Forest habitat types of Montana. U.S.D.A. Forest Service General Technical Report INT-34. Ogden, Utah. 174 pages.

Pylypec, B. 1986. The Kernen Prairie—A relict fescue grassland near Saskatoon, Saskatchewan. The Blue Jay 44: 222–231.

Pylypec, B. 1991. Impacts of fire on bird populations in a fescue prairie. Canadian Field-Naturalist 105: 346–349.

Pylypec, B., and **J.T. Romo.** in press. Long-term effects of burning *Festuca*- and *Stipa-Agropyron*-dominated grasslands. Journal of Range Management 56: In press.

Raby, S. 1966. Prairie fires in the North-West. Saskatchewan History 19: 81–99.

Redmann, R. E. 1978. Plant and soil water potentials following fire in a northern mixed grassland. Journal of Range Management 31: 443–445.

Redmann, R. E. 1991. Nitrogen losses to the atmosphere from grassland fires in Saskatchewan, Canada. International Journal of Wildland Fire 1: 239-244.

Redmann, R. E., J. T. Romo, B. Pylypec, and **E. A. Driver.** 1993. Impacts of burning on primary production of *Festuca* and *Stipa-Agropyron* grasslands in central Saskatchewan. American Midland Naturalist 130: 262–273.

Renken, R. B., and **J. J. Dinsmore**. 1987. Non-game bird communities on managed grasslands in North Dakota. Canadian Field-Naturalist 101: 551–557.

Romo, J. T., P. L. Grilz, R. E. Redmann, and **E. A. Driver.** 1993. Standing crop, biomass allocation patterns and soil-plant water relations in *Symphoricarpos occidentalis* Hook. following autumn or spring burning. American Midland Naturalist 130: 106–115.

Romo, J. T., P. L. Grilz, and **E. A. Driver.** 1990. Invasion of the Canadian Prairies by an exotic perennial. Blue Jay 48: 130–135.

Ross, R. L., and **H. E. Hunter.** 1976. Climax vegetation of Montana based on soils and climate. U.S.D.A. Soil Conservation Service. Bozeman, Montana. 64 pages.

Rowe, J. S., and **R. T. Coupland.** 1984. Vegetation of the Canadian plains. Prairie Forum 9: 231–248.

Russel, R. C. 1971. The Carlton Trail-The broad highway into the Saskatchewan from the Red River settlement. Prairie Books, The Western Producer, Saskatoon, Saskatchewan. 158 pages.

Seig, C. H., C. H. Flather, and **S. McCanny.** 1999. Recent biodiversity patterns in the Great Plains: Implications for restoration and management. Great Plains Research 9: 277–313.

Stickney, P. F. 1960. Range of rough fescue (*Festuca scabrella* Torr.) in Montana. Proceedings of the Montana Academy of Science 2: 12–17.

Stringer, P. W. 1973. An ecological study of grasslands in Banff, Jasper, and Waterton Lakes National Parks. Canadian Journal of Botany 51: 383–411.

Stueter, A. A., and **G. R. McPherson.** 1995. Fire as a physical stress. Pages 550-579 *in* Wildland plants-physiological ecology and developmental morphology. *Edited by* D. J. Bedunah and R. E. Sosebee. Society for Range Management, Denver, Colorado.

Swetnam, T. W., C. D. Allen, and **J. L. Betancourt.** 1999. Applied historical ecology: Using the past to manage for the future. Ecological Applications 9: 1189–1206.

Tisdale, E. W. 1947. The grasslands of the Southern Interior of British Columbia. Ecology 28: 346–382.

Toynbee, K. 1987. Prolific flowering year for plains rough fescue at the Kernen Prairie. Blue Jay 45: 142–143.

Trottier, G. C. 1986. Disruption of rough fescue, *Festuca hallii*, grassland by livestock grazing in Riding Mountain National Park, Manitoba. Canadian Field-Naturalist 100: 488–495.

Turner, M. G., W. H. Romme, R. H. Gardner, R. V. O'Neill, and **T. K. Kratz.** 1993. A revised concept of landscape equilibrium: Disturbance and stability on scaled landscapes. Landscape Ecology 8: 213–227.

Turner, M. G., R. H. Gardener, R. V. O'Neill, and **S. M. Pearson.** 1994a. Multiscale organization of landscape heterogeneity. Pages 73-79 *in* Volume II. Ecosystem management: Principles and applications. U.S.D.A. Forest Service General Technical Report PNW-GTR-318. Portland, Oregon. 376 pages.

Turner, M. G., W. H. Romme, and **R. H. Gardner.** 1994b. Landscape disturbance models and the long-term dynamics of natural areas. Natural Areas Journal 14: 3–11.

Umbanhowar, C. E. Jr. 1996. Recent fire history of the Northern Great Plains. American Midland Naturalist 135: 115–121.

Urban, D. L. 1994. Landscape ecology and ecosystem management. Pages 127-136 *in* Sustainable ecosystems: Implementing an ecological approach to land management. U.S.D.A. Forest Service General Technical Report RM-247. Fort Collins, Colorado. 363 pages.

West, N. E. 1993. Biodiversity of rangelands. Journal of Range Management 46: 2–13.

World Wildlife Fund. 1988. Prairie conservation action plan-1989-1994. World Wildlife Fund Canada, Toronto. 38 pages.

Wright, H. A., and **A. W. Bailey.** 1982. Fire ecology: United States and southern Canada. John Wiley and Sons, New York. 501 pages.

Received 11 February 2002
Accepted 2 July 2003

A Brief History of Purple Loosestrife, *Lythrum salicaria*, in Manitoba and its Status in 2001

CORY J. LINDGREN

Manitoba Purple Loosestrife Project, c/o Ducks Unlimited Canada, Box 1160, Stonewall, Manitoba R0C 2Z0 Canada

Lindgren, Cory J. 2003. A brief history of Purple Loosestrife, *Lythrum salicaria*, in Manitoba and its status in 2001. Canadian Field-Naturalist 117(1): 100–109.

Purple Loosestrife (*Lythrum salicaria* L.) has become recognized as an invasive alien plant having deleterious impacts on Manitoba's natural areas. The first herbarium specimen of Purple Loosestrife was collected in 1896 near Neepawa followed by infestations in 1944 at Lockport and in 1951 in Winnipeg. As of 1991 there were 38 known populations of Purple Loosestrife in Manitoba. By the fall of 2001, there were a known 492 populations covering an estimated 5575 ha of habitat. These data indicate a 13-fold increase in the number of Purple Loosestrife infestations between 1991 and 2001 in Manitoba. The majority of Purple Loosestrife (77.6%) was found in central Manitoba infesting 4324 ha. The Netley-Libau Marsh, located in central Manitoba, accounted for 26% of all Purple Loosestrife in Manitoba. Central Manitoba (42.6%) had the majority of all Purple Loosestrife infestations followed by the city of Winnipeg (41.4%), eastern Manitoba (9.9%) and western Manitoba (6.1%). Purple Loosestrife was commonly found in roadside ditches (46%), river banks (25%) and wetland habitats (10%). *Typha* spp., *Phalaris arundinacea* and *Carex* spp. were commonly associated with Purple Loosestrife infestations. Infestations ranged from one plant to thousands of plants. Of the infestations surveyed, 9% had over 1000 plants while 52% had under 100 plants.

Key Words: *Lythrum salicaria*, Purple Loosestrife, alien invasive, Manitoba, invaded habitats, status of infestation.

Invasive plants are those that have moved into a habitat and reproduced so aggressively that they displace some of the original components of the vegetative community (White et al. 1993), while an alien refers to a plant that did not originally occur in an area where it is now established (White et al. 1993). White et al. (1993) described Purple Loosestrife (*Lythrum salicaria* L.) as an invasive alien wetland species that presents a serious threat to the plant communities of natural areas in Canada. While many invasive alien plants have little impact on our natural areas, Purple Loosestrife is implicated in causing deleterious impacts resulting in both environmental and economic costs (Pimentel et al. 2001; Stein and Flack 1997).

The Government of Canada (2001), responding to an opinion of researchers that invasive aquatic species are a factor in the extinction of native aquatic species second only to habitat destruction (Wilcove et al. 1998), estimates that in the Great Lakes and St. Lawrence River Basins in Canada, $500 million is spent each year on efforts to control invasive species. Studies in the United States of America report that alien species are implicated in the decline of 42% of threatened or endangered species and that 79 alien species have cost the USA economy an estimated $97 billion from 1906 to 1991 (Stein and Flack 1997). In the United States, it is estimated that Purple Loosestrife alone costs $45 million per year in control and forage losses (Pimentel et al. 2001). In Manitoba, alien aquatic invasive species are recognized as a threat to Manitoba's ecosystems (Manitoba Conservation 2001*; Ralley 2002); however, no costs associated with loss of habitat/biological diversity or with providing control programs are available.

Scudder (2002) provides numerous examples of the impact biological invaders have had on biodiversity, ecosystem function, economics and human health. It has been suggested that invasive alien species can be particularly deleterious to natural areas and native species that are already under stress from human impacts such as habitat destruction, degradation, or pollution (Stein and Flack 1997). In some countries, biological invasions have surpassed habitat destruction as the prime threat to native biodiversity. For example, in New Zealand biological invasions are the main causes attributed to the loss of native biodiversity, not the loss of habitat or the direct effects of people (Clout 2001).

Purple Loosestrife is a European plant that has naturalized in North America (Scoggan 1957). It is believed that Purple Loosestrife was accidentally introduced into North America in the early 1800s in the ballast of ships arriving on the east coast of North America from European destinations (Thompson et al. 1987) as well as by intentional introductions by beekeepers, by immigrants as a medicinal herb, and through seeds attached to wool on sheep imported from Europe (Mal et al. 1992).

Purple Loosestrife has the ability to invade natural areas and replace native plant species that provide food, shelter and breeding areas for wildlife species. Mal et al. (1992) noted that in areas where Purple

*See Documents Cited section

Loosestrife has invaded, wildlife species are in decline and further demonstrated that *Lythrum salicaria* is capable of replacing the native wetland species *Typha angustifolia* within four years. One of the earliest reports of Purple Loosestrife replacing native plant communities in Canada was from the St. Lawrence floodplain near Montreal (Fernald 1940). Mal et al. (1992) provided a historical review of the introduction of Purple Loosestrife into Canada noting that the first herbarium specimen was collected between 1850 and 1874 at Lotbiniere, Quebec and *L. salicaria* subsequently spread through habitat altered by agricultural settlement, military activities, and the construction of canal, highway and railway networks. It has been estimated that Purple Loosestrife is now responsible for the loss of more natural habitat across North America than current human development pressure (Mal et al. 1992). The objective of this paper is to document the status of the alien invasive plant Purple Loosestrife in Manitoba to 2001, describe historical accounts, and discuss likely vectors of introduction. These data can then be used to implement and direct weed management efforts.

Methods

Data on Purple Loosestrife infestations in Manitoba were collected between 1992 and 2001 as part of the ongoing Manitoba Purple Loosestrife Project (MPLP). The MPLP is an environmental stewardship coalition formed in 1992 and composed of the Canadian Wildlife Service (Environment Canada), City of Winnipeg Parks and Natural Areas, Ducks Unlimited Canada, Delta Waterfowl, Manitoba Conservation, Manitoba Naturalists Society, and the Manitoba Weed Supervisors Association.

When possible, infestations were verified by MPLP project staff. Aerial surveys of the Delta Marsh, Big Grass Marsh, Oak Hammock Marsh, Minnedosa pothole region, and the Red River were flown on 18 August 1999. Aerial and airboat surveys of the Netley-Libau Marsh occurred in 1999 and in 2001. The Seine River and Sturgeon Creek in Winnipeg were surveyed in 1998 while the Red and Assiniboine Rivers were surveyed in 1992, 1993, and again in 1998. Manitoba weed supervisors have provided annual Purple Loosestrife distributional maps for their weed districts since 1992.

A hand-held GPS unit (Eagle Explorer, Lowrance Eagle Canada, Mississauga, Ontario) was used to collect geographic positions of Purple Loosestrife infestations whenever possible. Data were entered into a Microsoft Excel spreadsheet. Data fields included region, geographic location, year added to the database, latitude and longitude, Universal Transverse Mercater coordinates, weed district, weed supervisor, habitat description, estimated number of plants, an estimate of the area infested (m^2), and information on any past management/control. The two most commonly occurring plants associated with the *L. salicaria* infestation were recorded, with the most dominant (based upon stem numbers) being recorded as a 1st associate. Garden plantings were not included in the inventory. "Arcview" GIS (Environmental Systems Research Institute, Inc., Redlands, California, USA) was used to analyze data geographically.

To aid in data retrieval and analysis, Manitoba was divided into the following four regions: Winnipeg, Central Manitoba, Eastern Manitoba and Western Manitoba. The western region is bordered by the Saskatchewan border on the west and provincial highway # 5 to the east. The central region is bordered by provincial highway #5 to the west and provincial highway #75 and #59 to the east. The eastern region is bordered by provincial highway #75 and #59 on the west and the Ontario border to the east. The Winnipeg region is composed of the area within the perimeter highway.

Results and Discussion

Population Size and Trends

As of the fall of 2001, there were 492 known Purple Loosestrife infestations in Manitoba (Figure 1) with an estimated 5575.1 ha of Purple Loosestrife (Table 1). There is no doubt that some infestations were not discovered, so this is a conservative estimate. The number of Purple Loosestrife infestations was found to be greatest in the central, Winnipeg, western and eastern regions of Manitoba (Table 1). In 1991 there were 38 known populations of Purple Loosestrife in Manitoba with the majority in the watersheds of the Red and Assiniboine Rivers (Ottenbreit 1991). Comparison of these data, shows that there has been a 13-fold increase in the number of Purple Loosestrife infestations in Manitoba

TABLE 1. Regions of Manitoba with Purple Loosestrife, 2001. The western region is bordered by the Saskatchewan border and provincial highway # 5; the central region is bordered by provincial highway #5 and provincial highway #75; the eastern region is bordered by provincial highway #75 and the Ontario border; the Winnipeg region is composed of the area within the perimeter highway.

Regions	Number of Known Infestations	Estimated Extent of Purple Loosestrife (ha)
Central	210 (42.6 %)	4 324.9 (77.6%)
Winnipeg	203 (41.4 %)	537.6 (9.6%)
Eastern	49 (9.9 %)	434.0 (7.8 %)
Western	30 (6.1 %)	278.6 (5.0 %)
TOTAL	492	5575.1

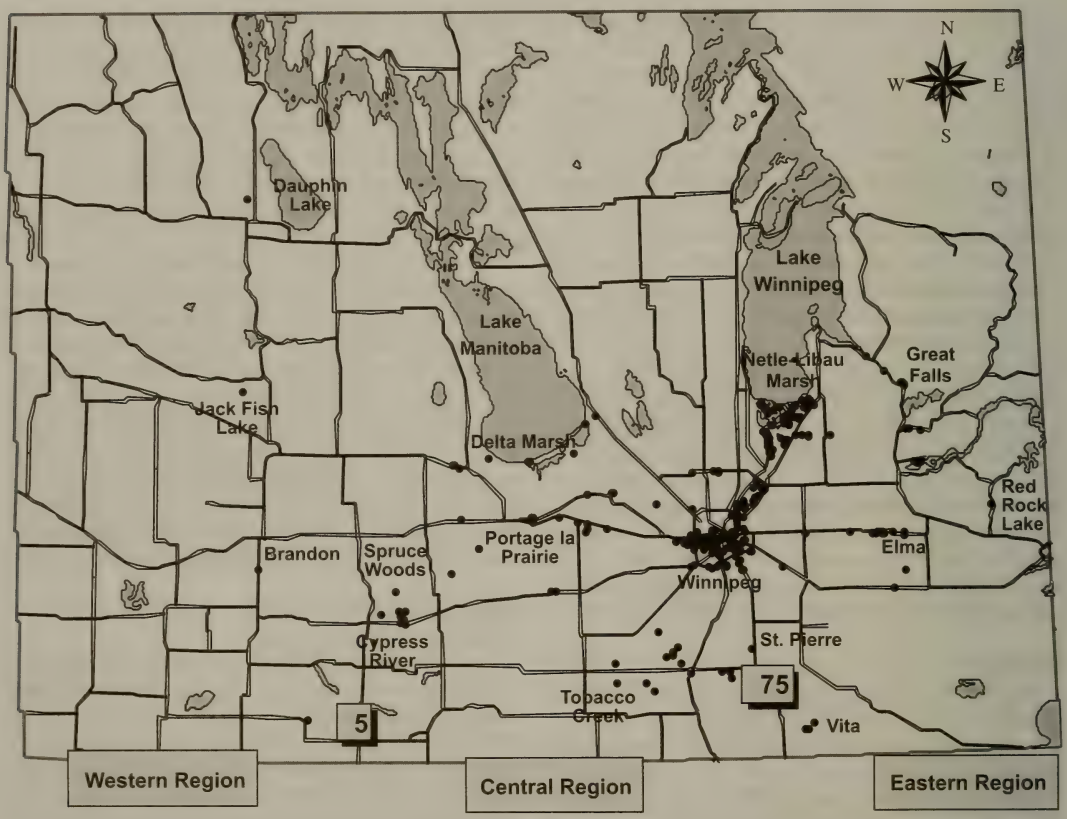


FIGURE 1. Dots indicate the 492 known Purple Loosestrife infestations in southern Manitoba as of the fall of 2001. Numerous infestations are found in the Netley-Libau Marsh, in the city of Winnipeg, and Cypress River area.

between 1991 and 2001 (10-year period). Central Manitoba, which includes the Netley-Libau Marsh, accounted for 4324 ha (77.5%) of Purple Loosestrife. The Netley-Libau Marsh (a candidate Manitoba Heritage Marsh and Canadian Important Bird Area) accounted for the majority of Purple Loosestrife in the central region while the Assiniboine River accounted for the majority of Purple Loosestrife infestations within the city of Winnipeg.

The size of Purple Loosestrife infestations ranged from one plant to thousands of plants. The largest single infestations were found along the Winnipeg River near Great Falls, along the Assiniboine River within the city of Winnipeg, in the Netley-Libau Marsh, and on private land off Main Street in West. St. Paul. Sites in Manitoba with infestations of over 1000 plants represented under 9% of the total number of sites while over 50% of the infestations had under 100 plants (Table 2). The potential to control these smaller populations of under 100 plants with an aggressive weed control program is high. This suggests that there is opportunity to control or eradicate over 50% of the Purple Loosestrife infestations presently found in Manitoba.

The Manitoba Weed Supervisors Association (MWSA) provided Purple Loosestrife distributional maps for weed districts with Purple Loosestrife infestations. The MWSA represents 34 weed control districts in Manitoba composed of about 70 municipal corporations. Of the 34 weed districts in Manitoba, 16 were found to have at least one Purple Loosestrife infestation (Table 3). Three additional districts (Roland, Grey and Woodlands) to which the MWSA provide contract services also were found to have Purple Loosestrife.

TABLE 2. Percentage of Purple Loosestrife infestations in Manitoba classified by number of plants in an infestation based on data from 432 sites in southern Manitoba 2001.

Number of Plants	Infestations
> 10 000	3.4 %
9999 – 5000	1.6 %
4999 – 1000	3.4 %
999 - 500	23.3 %
499 - 100	15.5 %
99 – 10	20.6 %
< 10	31.9 %

TABLE 3. Manitoba weed districts with Purple Loosestrife infestations.

Selkirk	Piney Stuartburn
Macdonald	Agassiz
Montcalm Morris	Cornwalis
Rosser Rockwood	Portage la Prairie
Westbourne	Dauphin Ochre River
South Norfolk Victoria	Glenboro South Cypress
Weed District #4	Red River
Springfield Tache	Reynolds Whitemouth
Grey	Roland
Woodlands	

Plants Associated with *Lythrum* infestations

Fourteen plant species were found associated with Purple Loosestrife infestations in Manitoba. *Typha* spp. (includes *T. latifolia*, *T. angustifolia*, and the hybrid *T.* x *glauca*), *Phalaris arundinacea,* and *Carex* spp. were the three most commonly occurring associates (Table 4). Thompson et al. (1987) also reported the identical three plant species as being the most common associates of Purple Loosestrife in his inventory of 45 sites in Northeast, Mideast, and Northwest United States and southern Canada. Associated sedge species in Manitoba included *Carex atherodes*, *C. lanuginosa*, and *C. rostrata.* Additional plant species associated with Purple Loosestrife infestations but not a first or second associated species included *Potentilla anserina, Lycopus americanus, Anemone canadensis, Vicia americana, Lysimachia thyrsiflora, Mentha arvensis, Aster laevis,* and *Galeopsis tetrahit* (Lindgren 2000). Some of the associated plant species found in this survey are in themselves recognized as alien invasive species including Flowering Rush (*Butomus umbellatus* L.) and Reed Canary Grass (*Phalaris arundinacea* L.) (White et al. 1993). Other associated species such as the hybrid *Typha* spp. (*T.* × *glauca*) and *Phragmites australis* are recognized as invasive species of concern by wetland managers and have become dominant plants lowering overall biological diversity in natural areas such as the Delta Marsh and Netley-Libau Marsh in Manitoba.

Invaded Habitats

Infestations were found highest in roadside ditches (46%), followed by riverbanks (25%) and wetlands (10%) (Table 5). In Minnesota, high percentages of the Purple Loosestrife infestations were also found in roadside ditches (15%), wetlands (29%) and along lakeshores (32%) (Skinner et al. 1994). There were a number of lakes and rivers found to have Purple Loosestrife infestations (Table 6).

The number of infestations in roadside ditches is likely to be higher than reported here, for many Purple Loosestrife infestations along roads go undetected. First, roadside ditches are subjected to annual weed control programs which either directly or indirectly target and control Purple Loosestrife. Second, haying operations along roadsides remove Purple Loosestrife prior to flower blooming stage. However, in wet years such as 2001, haying along roadside ditches was delayed well into September hence numerous Purple Loosestrife infestations were detected and added to our database. Manitoba roadside ditches with significant (more than 1000 plants) Purple Loosestrife infestations included provincial highway #59 from the Birds Hill Park to Grand Beach Provincial Park, provincial highway #15 from Nourse through the Sandilands Provincial Forest to Elma, and along provincial highway #2 near Haywood.

History of an Invasion

The first records of *L. salicaria* in Manitoba were collected from Neepawa in 1896 (Scoggan 1957), at Lockport (about 10 miles northeast of Winnipeg) on

TABLE 4. Plant species associated with Purple Loosestrife infestations from 96 sites in Manitoba. Data represent first and second dominant plant species based on stem numbers at a site and do not reflect all plant species present at a site.

Species	% 1st Association	% 2nd Association
Typha spp., cattail	52 %	12 %
Carex spp., sedge	14 %	14 %
Phalaris arundinacea, Reed Canary Grass	11 %	8 %
Phragmites australis, Giant Reed Grass	6 %	16 %
Salix spp., willow	5 %	12 %
Juncus spp., spike rush	5 %	5 %
Unknown grasses	2 %	1 %
Scolochloa festucacea, Whitetop	1 %	4 %
Butomus umbellatus, Flowering Rush	0 %	1 %
Equisetum fluviatile, Horsetail	0 %	1 %
Cirsium spp., thistle	0 %	1 %
Rumex occidentalis, Western Dock	0 %	12 %
Polygonum spp., smartweed	0 %	5 %
Scirpus spp., bulrush	0 %	3 %

TABLE 5: Habitat types invaded by Purple Loosestrife in Manitoba based upon 492 sites in 2001. Note that garden plantings were not included in the inventory.

Habitat	Western	Central	Eastern	Winnipeg	Total (%)
Roadside ditch	13	125	33	56	226 (46%)
River bank	3	15	7	100	125 (25%)
Marsh/wetland	6	42	1	3	52 (10%)
Creek	2	2	1	15	24 (5 %)
Lake shore	2	11	3	3	19 (4 %)
Retention pond	0	0	0	13	13 (3 %)
Dugout	0	2	1	0	3 (1 %)
Railway track	0	0	0	7	7 (1 %)
Terrestrial	1	4	0	3	8 (1 %)
Pond	1	3	1	0	4 (1%)
Quarry	0	0	1	0	1 (.2 %)
Lagoon	0	1	0	0	1 (.2 %)
Garbage dump	0	0	1	0	1 (.2 %)

TABLE 6. Manitoba waterbodies with Purple Loosestrife infestations as of 2001.

Manitoba Waterbody	Location of Largest Infestation
Winnipeg River	Great Falls
Red River	Netley-Libau Marsh
Assiniboine River	Winnipeg
Seine River	Winnipeg
Cypress River	Park Road
Whitemud River	Whitemud Farms
La Salle River	Sanford
Lake Winnipeg	Netley-Libau Marsh
Lake Manitoba	Delta Marsh
DeGueldres Lake	East end of lake
Crescent Lake	Portage la Prairie
Killarney Lake	Killarney
Red Rock Lake	Camp Whisky Jack
Betula Lake	Shoreline
Jackfish Lake	Islands near middle
Oak Lake	South end of marsh

the Red River in 1944, and within the Winnipeg area in Fort Garry in 1951. The herbarium record from Neepawa may have been the result of early European settlers bringing the plant with them into Manitoba as a medicinal plant. By the end of the 1950s Purple Loosestrife infestations were found in Delta Marsh, Otterburne, Fannystelle, and on the Cypress River (Ottenbreit 1991). By the late 1980s Purple Loosestrife had become a concern with various conservation agencies in Manitoba including the City of Winnipeg, Canadian Wildlife Service and Ducks Unlimited Canada. These data indicate about a 45-year lag time between the first infestations and the time Purple Loosestrife became recognized as a threat to Manitoba's natural areas.

Central Region

Delta Marsh. The Delta Marsh is one of the largest (15 000 ha) freshwater marshes in North America located on the south shore of Lake Manitoba (50°11′N, 98°19′W) (Sandilands et al. 2000). Walker (1965) studied the vegetation of Delta Marsh from 1959 to 1961 making no mention of the presence of *L. salicaria* within her vegetation sampling transects. It may be assumed that there was no Purple Loosestrife in the Delta Marsh prior to 1961. In the early 1960s local residents began introducing Purple Loosestrife into the Delta Marsh area as a landscape ornamental. At this time others already recognized it as an invasive plant and were advising against its introduction in the Delta Marsh area (J. Shay, personal communication, 1999). Shortly after these introductions, the plant escaped and was described as a weed problem in the Delta Marsh by Friesen (1966), who reported the weed replacing native plant species important for waterfowl. Friesen (1966), who conducted a number of herbicide trials on Purple Loosestrife in the Delta Marsh between 1961 and 1964, noted that Purple Loosestrife represents an important weed problem in Manitoba in that it replaces native plant species important for waterfowl. Over the 1960s and 1970s students working at Delta Marsh were tasked with digging out Purple Loosestrife when time permitted. More recently, Murkin et al. (2000) reported Purple Loosestrife as part of the Delta Marsh plant community that has appeared to stabilize over the last 25 years.

Netley-Libau Marsh. The Netley-Libau Marshes are located in the south basin of Lake Winnipeg and include 24 381 hectares of upland and wetland habitats (Verbiwski 1986*). The Netley-Libau Marsh was found to have 1452 ha or 34% of the total area infested in the central region and represented 26% of the total area infested in the entire province of Manitoba. A vegetation survey carried out by Hinks and Fryer (1936) under the authority of the Winnipeg Game and Fish Association examined 13 waterbodies within the Netley-Libau Marsh and the

survey did not note any Purple Loosestrife infestations at that time. Forty years later, Verbiwski (1986*) conducted a vegetation survey of the marsh and reported that by 1979 Purple Loosestrife was a plant of common occurrence within the marshes.

Based upon reports of Purple Loosestrife populations located on the Red River near Lockport in 1944 (Ottenbreit 1991), Purple Loosestrife most likely established in the Netley-Libau Marshes sometime in the late 1940s to early 1950s. The Red River, which flows from Lockport into the Netley-Libau Marshes, may have served as one vector for Purple Loosestrife seed dispersal. Purple Loosestrife in the Netley-Libau Marsh can also be attributed to human intervention. Individuals in the area believed the flowering spikes would be a colorful addition to the marsh plant community and in the 1960s began spreading Purple Loosestrife seed through areas of marsh near the End of Main Street area and between Goldeye Creek and Netley Creek (Doug Schindler, personal communication, August 2001). The deleterious impacts of Purple Loosestrife were not recognized by these individuals at this time.

By the early 1990s Purple Loosestrife could be found throughout the Netley-Libau Marsh complex with the majority of the larger infestations found on the Libau side of the marsh off Boulton and Anderson roads, and in Folster's Lake. The largest infestation in the marsh, and perhaps in all of Manitoba, is located between Lake Winnipeg and Hardmans Lake in the Netley Marsh Game Bird Refuge, which is estimated to have well over 10 000 plants.

Winnipeg Region. Riparian areas in the city of Winnipeg such as the Red River, Assiniboine River and Seinne Rivers all were found to have significant Purple Loosestrife populations that are most likely the result of garden escapes. Of the 204 infestations found in the Winnipeg area, 40% (N=82) were found along the Assiniboine River and 7% (N=15) along the Seinne River. Surveys conducted in 1992 and 1993 indicated that the Red River, as it flows through Winnipeg, has numerous infestations along its shorelines and on the islands. Water levels along the Assiniboine River have generally been high through the late 1990s and many of these Purple Loosestrife infestations recorded in 1992 and 1993 have not emerged through the later part of the 1990s. It is predicted that when Manitoba experiences low water conditions these Purple Loosestrife infestations along the Assiniboine River will emerge. Infestations were found along the Red River downstream (north) from where the Assiniboine and Red Rivers meet (The Forks) while no infestations were found on the Red River upstream (south) of The Forks. These findings suggest that seeds are being transported from the Assiniboine River into the Red River.

In the city of Winnipeg numerous storm water retention ponds have stands of Purple Loosestrife (Table 7). These infestations are the results of escapes from surrounding garden plantings. In south Winnipeg large stands currently exist around retention ponds in the Southdale drainage area including ponds adjacent to Edgewater and Lakewood Parks. Prior to the early 1990s, Purple Loosestrife was intentionally planted into many areas of Winnipeg such as Assiniboine Park and Kings Park as a landscape ornamental (these plantings have since been removed). Railway traffic in Winnipeg was also found to be a vector for Purple Loosestrife dispersal. Purple Loosestrife was found along railway tracks, growing between railway tracks, as well as in the ditches along railway lines near Ellice Avenue, Border Street, Valour Road and Otter Avenue. These infestations are most likely the result of seeds being introduced by railcars and will continue to be a source of seeds until control measures are introduced.

Eastern Region

Between the towns of Nourse and Elma there are numerous Purple Loosestrife infestations along provincial highway #15. These are small scattered infestations that were found in ditches on both sides of the highway #15 running for several kilometers. Infestations were found along Hazel Creek and along the Brokenhead River as they intersect provincial highway #15. In the eastern region a large infestation was found along the Winnipeg River near the town of Great Falls beginning on the west shoreline at the Manitoba Hydro generating station.

Whiteshell Provincial Park. One of the first known infestations in eastern Manitoba was reported in 1995 on Red Rock Lake at Camp Whiskey Jack in the Whiteshell Provincial Park. Camp Whiskey Jack is on the eastern shoreline of Red Rock Lake and was at one time a provincial entomology camp and it is believed that Purple Loosestrife may have been intentionally planted at the camp (Chris Atkin, personal communication, 1995). A second infestation in the Whiteshell Provincial Park was found at Betula Lake in 2001. The Whiteshell Provincial Park has numerous waterbodies and pristine natural areas and at present very few Purple Loosestrife infestations.

Western Region

Cypress River. Numerous infestations of Purple Loosestrife were found in 1992 in the Cypress River area along roadside ditches leading into Spruce Woods Provincial Park and in several small wetlands on private agricultural lands. Significant infestations were found along the Cypress River and in oxbows of the river north of provincial highway #2. This region is also known as the prairie pothole region and these small wetlands are of significant importance to North America's waterfowl production.

TABLE 7. Winnipeg Retention Ponds with Purple Loosestrife as of the fall of 2001.

Pond Number	Description	Winnipeg Drainage Area
4-2	Bunn's Creek Pond	Bunns Creek
4-5	Morley Kare Park (Devonshire Dr.)	Bunns Creek
5-8	Edgewater Park	Southdale
5-5	Lakewood Park West Pond	Southdale
5-6	Lakewood Park East Pond	Southdale
5-15	Island Lakes Drive	South St. Boniface
6-17	Scurfield Park	Fort Garry
6-12	Grandmont Park	Fort Garry
6-13	Ducharme Park	Fort Garry
6-18	Van Walleghem Park	Tuxedo
6-7	Lake Lindero – Thelma J. Call Park	Fort Garry
6-9	Governor Lake – A.A. Leach Park	Fort Garry
6-10	Baldry Creek Park (Fort Richmond)	South St. Vital

Purple Loosestrife has invaded these prairie potholes and in turn may have an impact on waterfowl breeding in the Cypress River area and provide seed for further infestations to the prairie pothole region.

Provincial Parks and Special Areas

Purple Loosestrife has been located in a number of provincial parks in Manitoba, including Spruce Woods Provincial Park, Agassiz Provincial Forest, Sandilands Provincial Park, and the Whiteshell Provincial Park (Table 8). Purple Loosestrife was also found in the Libau Ecological Reserve. Thompson et al. (1987) documents that Purple Loosestrife can have a severe impact on parks and conservation areas, with over 190 000 ha of habitat being lost in the USA to Purple Loosestrife (prior to 1987).

Impact of 1997 Flood

In the spring of 1997 southern Manitoba suffered one of the worst floods in its history along the Red River Basin (International Joint Commission 2000). In attempts to mitigate future flooding many areas of Manitoba built ring dykes around towns and private residences. As a result of the transfer of soils and general disturbance, Purple Loosestrife was introduced into new sites such as the dyke ditch in Rosenort, Manitoba. Prior to the 1997 flood there was no Purple Loosestrife in Rosenort (Dave Knutt, personal communication, June 2001). The impacts of the 1997 flood on the dispersal of other invasive weed species is beginning to emerge, with new populations of invasive plant species such as Yellow Nutsedge *(Cyperus esculentus)* and Purple Nutsedge *(Cyperus rotundus)* being discovered (Dave Knutt, personal communication, June 2001). The nutsedges are classed among the world's worst weeds due to the difficulty in controlling the tubers or "nuts" produced on the rhizomes (Province of British Columbia 2001*).

Lythrum Cultivars

There are a number of examples of *Lythrum* spp. escaping from garden settings in Manitoba. South of the city of Brandon a stand of Purple Loosestrife can be found along a small creek intersecting Ferguson Road where the plant escaped from a previous landowner who grew Purple Loosestrife for commercial use in cut dry-flower arrangements (Brad Moorehead, MWSA, personal communication, August 2000). Garden escapes in the Rural Municipality of Morris have invaded roadside ditches as well, infesting at least 12 km of the Tobacco Creek Drain, which drains into the Morris River. Regions of Manitoba continue to be threatened by garden *Lythrum* species. For example, as of 2002, gardens in eastern Manitoba near the town of Elma had numerous plantings of Purple Loosestrife, some composed of long hedgerows of 20 or more plants which threaten to spread to the Whiteshell River and further into the Whiteshell Provincial Park.

The horticultural industry has been a recognized vector for the spread and proliferation of Purple Loosestrife with the introduction of numerous

TABLE 8. Manitoba Provincial Parks and Special Areas with Purple Loosestrife as of 2001.

Provincial Park	Area
Spruce Woods Provincial Park	DeGueldres Lake
Whiteshell Provincial Park	Red Rock Lake & Betula Lake
Agassiz Provincial Park	Provincial Highway #15
Sandilands Provincial Park	Spruce Siding
Libau Ecological Reserve	Provincial Highway #317

Lythrum cultivars, some developed in Manitoba, as well as the sale of wild *Lythrum salicaria*.There are numerous cultivated varieties of Purple Loosestrife. Mal et al. (1992) provided a list of 12 named cultivars of Purple Loosestrife in the Agriculture Canada Herbarium in Ottawa, while Skinner et al. (1994) provided a list of 25 horticultural cultivars under cultivation in the United States. In 1937, Agriculture Canada's Experimental Farm in Morden, Manitoba, introduced the cultivar Morden Pink and in 1967 announced that more home gardeners than ever were growing *Lythrum* as a result of Morden Pink (Harp and Collicutt 1967). The Morden station introduced two additional cultivars, Morden Gleam in 1953 and Morden Rose in 1954, and reported that Lythrums were ideal perennials for the home garden and naturalized areas (Harp and Collicutt 1967). Agriculture Canada (Harp and Collicutt 1967) did not report on seed production but indicated new plants are easy to start from cuttings.

Prior to the early 1990s Purple Loosestrife cultivars were accepted as sterile by the nursery trade; however, Ottenbreit (1991) countered that there never was any scientific documentation that established any of the cultivars as sterile. Subsequent research carried out in the early 1990s indicated that *Lythrum* cultivars were not sterile and contributed to the spread of Purple Loosestrife (Ottenbreit and Staniforth 1994; Anderson and Ascher 1993; Lindgren and Clay 1993). In Manitoba, Purple Loosestrife infestations along the Assiniboine River, Red River, Winnipeg River, Delta Marsh, Red Rock Lake, Portage la Prairie, Tobacco Creek, and the Northumberland Drain are most likely the result of garden cultivar escapes.

Controls

The Manitoba Noxious Weed Act

Purple Loosestrife has been on the Manitoba Noxious Weed Act since the early 1980s. However, the listing did not include any genus or species information. Confusion and questions then arose — are the garden varieties of Purple Loosestrife considered noxious weeds, does Purple Loosestrife refer only to the alien invasive *Lythrum salicaria*, or are all plants in the genus *Lythrum* considered noxious weeds? From the 1950s to the mid-1990s horticultural operations sold a variety of *Lythrum* cultivars suggesting that the Manitoba Noxious Weed Act referred only to the alien invasive *L. salicaria*. Many operations were also found selling the alien invasive *L. salicaria*, unaware it was Purple Loosestrife. Subsequently, the Manitoba Noxious Weeds Act was revised in March of 1996 so that Purple Loosestrife (*Lythrum salicaria*) as well as all cultivars of Purple Loosestrife are now considered noxious weeds in Manitoba and individuals can be fined for selling or planting loosestrife.

The reluctance of the greenhouse growers, landscapers and nurseryman to halt the sale of Purple Loosestrife cultivars was economically driven. Over the years, the horticultural trade reported that Purple Loosestrife had been one of their number-one selling perennials in Manitoba. However, after an educational campaign in the early 1990s, the horticultural industry in Manitoba responded proactively, and most, if not all, commercial operators no longer retailed any variety of *Lythrum* by 1995. One of the first companies was T & T Seeds of Winnipeg, which dedicated a page in their annual seed catalog to promoting the use of environmentally safe alternatives to Purple Loosestrife. A survey was conducted by the MPLP in Winnipeg in May of 1995 to determine the extent to which *Lythrum* varieties were being sold. Horticultural operators were unaware they were being surveyed (N=30) and not one was found to be retailing any varieties of *Lythrum*. These results demonstrate the effectiveness and importance of educational campaigns in an overall alien invasive species program.

Globalization and Challenges

As we move away from traditional economies and towards globalized economies with rapid transglobal movement of materials, the scale of exotic species introductions will only increase. It is the overall increase in human activities that is increasing the spread of alien species worldwide (Pimentel et al. 2001). The increased proliferation of the internet has provided access to markets previously unavailable, for example, Purple Loosestrife seed was found available on Ebay in the summer of 2001. Increased access to TV programs such as the Weather Network, which has promoted the use of Purple Loosestrife in garden landscaping, poses a challenge to the management of alien invasive species. Additional challenges include large box outlets such as Home Depot, which was found retailing Purple Loosestrife in British Columbia in 2001 (Province of British Columbia 2001*).

Purple Loosestrife is recognized by White et al. (1993) as an invasive alien weed species that threatens the ecological integrity of our natural areas. Data presented here demonstrate that from 1991 to 2001 there has been a 13-fold increase in the number of known Purple Loosestrife infestations in Manitoba. If Purple Loosestrife is not managed, an additional 13-fold increase (or higher) may be expected over the next 10-year period resulting in at least 6396 infestations by the year 2011. However, it should be possible to control or eradicate the majority of the Purple Loosestrife infestations currently found in Manitoba.

Larger infestations (more than 100 plants) may be managed through a classic biological control program. Post-release monitoring data compiled in Manitoba have indicated that the beetle *Galerucella*

calmariensis is an effective biological control agent against Purple Loosestrife resulting in control within 3 to 4 years in some cases (Lindgren 2000). Many of the infestations detected in this survey have received biological control releases. Smaller infestations (less than 100 plants) can potentially be managed through herbicide applications and mechanical control. High priority must be placed on keeping Purple Loosestrife out of uninfested watersheds. This may best be accomplished by fostering awareness that will lead to individuals being able to identify the plant and to take action to destroy small founder infestations.

Acknowledgments

The MPLP would like to gratefully thank the Murphy Foundation, the Sustainable Development Innovations Fund, EcoAction 2000, Ducks Unlimited Canada, Manitoba Conservation, Manitoba Hydro, Urban Green Team, Canadian Wildlife Service, and the City of Winnipeg for funding support. Office space is kindly donated in-kind by Ducks Unlimited Canada at Oak Hammock Marsh, Manitoba. The MPLP is a non-profit coalition composed of Agriculture Canada, City of Winnipeg Parks and Natural Areas, Canadian Wildlife Service, Ducks Unlimited Canada, Delta Waterfowl, Manitoba Conservation, Manitoba Agriculture, Manitoba Naturalists Society, and the Manitoba Weed Supervisors Association (MWSA). I thank members of the MWSA who provided distributional maps and are working to control Purple Loosestrife across Manitoba.

Documents Cited (marked * in text)

Manitoba Conservation. 2001. Building a Sustainable Future: Water: A Proposed Strategic Plan for Manitoba. A Discussion Paper. October 2001. Manitoba Conservation. Winnipeg. 21 pages.

Province of British Columbia. 2001. Yellow & Purple Nutsedge. Weed Alert http://www.agf.gov.bc.ca/croplive/cropprot/nutsedge.htm. Viewed November 2001.

Verbiwski, B. N. 1986. Netley-Libau Marshes Resource Development and Management Proposal. April 1986. Manitoba Natural Resources, Wildlife Branch Report. 190 pages.

Literature Cited

Anderson, N. O., and **P. D. Ascher.** 1993. Male and female fertility of loosestrife (*Lythrum*) cultivars. Journal of American Society for Horticultural Science 118: 851–858.

Clout, M. 2001. Where protection is not enough: active conservation in New Zealand. Trends in Ecology & Evolution 16: 415–416.

Fernald, M. L. 1940. The problem of conserving rare native plants. Annual Report of the Smithsonian Institution (1939): 375–391.

Friesen, G. 1966. Aquatic weed control studies in Manitoba. North Central Weed Control Conference: 21: 42–43.

Gaudet, C. L. and **P. A. Keddy.** 1988. A comparative approach to predicting competitive ability from plant traits. Nature 334: 242–243.

Government of Canada. 2001. Report of the Commissioner of the Environment and Sustainable Development to the House of Commons. Minister of Public Works and Government Services Canada.

Harp, H. F., and **L. M. Collicutt.** 1967. *Lythrums* for home gardens. Minister of Supply and Services, Communications Branch, Agriculture Canada, Ottawa.

Hinks, D., and **R. Fryer.** 1936. Aquatic plant survey 1936. Manitoba Department of Mines and Natural Resources Government Report. 32 pages.

International Joint Commission. 2000. Living with the Red. A report to the Governments of Canada and the United States on Reducing Flood Impacts in the Red River Basin. International Joint Commission. 82 pages.

Lindgren, C. J. 2000. Performance of a biological control agent, *Galerucella calmariensis* L. (Coleoptera: Chrysomelidae) on Purple Loosestrife *Lythrum salicaria* L. in Southern Manitoba (1993-1998). Pages 367-382 *in* Proceedings of the X International Symposium of Biological Control of Weeds 4-14 July 1999. *Edited by* Neal R. Spencer. Montana State University, Bozeman, Montana.

Lindgren, C. J. and **R. T. Clay.** 1993. Fertility of 'Morden Pink' *Lythrum virgatum* L. transplanted into wild stands of *L. salicaria* L. in Manitoba. HortScience 28: 954.

Mal, T. K., J. Lovett-Doust, L. Lovett-Doust, and **G. A. Mulligan.** 1992. The biology of Canadian weeds 100. *Lythrum salicaria.* Canadian Journal of Plant Science 72: 1305–1330.

Murkin, H. R., A. G. van der Valk, and **W. R. Clark.** 2000. Prairie Wetland Ecology; The Contribution of the Marsh Ecology Research Program. Iowa State University Press. Ames, Iowa. 413 pages.

Ottenbreit, K. 1991. The distribution, reproductive biology, and morphology of *Lythrum* species, hybrids and cultivars in Manitoba. M.Sc thesis. University of Manitoba, Winnipeg, Manitoba. 145 pages.

Ottenbreit, K., and **R. J. Staniforth.** 1994. Crossability of naturalized and cultivated *Lythrum* taxa. Canadian Journal of Botany 72: 337–341.

Pimentel, D., S. McNair, J. Janecka, J. Wightman, C. Simmonds, C. O'Connell, E. Wong, L. Russel, J. Zern, T. Aquino, and **T. Tsomondo.** 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agriculture, Ecosystems and Environment 84: 1–20.

Ralley, W. 2002. Alien aquatic species in Manitoba: present and threatening. Pages 93-102 *in* Alien Invaders in Canada's Waters, Wetlands and Forests. *Edited by* R. Claudi, P. Nantel and E. Muckle-Jeffs. Canadian Forest Service, Natural Resources Canada, Ottawa.

Sandilands, K. A., B. J. Hann, and **L. Gordon Goldsborough.** 2000. The impact of nutrients and submersed macrophytes on invertebrates in a prairie wetland, Delta Marsh, Manitoba. Arch. Hydrobiology 148: 441–459.

Scoggan, H. J. 1957. Flora of Manitoba. National Museum of Canada. Bulletin 140. 619 pages.

Scudder, G. E. 2002. Alien invaders: an introduction. Pages 15-18 *in* Alien invaders in canada's waters, wetlands and forests. *Edited by* R. Claudi, P. Nantel, and E. Muckle-Jeffs. Canadian Forest Service, Natural Resources Canada, Ottawa.

Skinner, L., W. J. Rendall, and **E. L. Fuge.** 1994. Minnesota's Purple Loosestrife Program: History, Findings and Management Recommendations. Minnesota Department of Natural Resources, Division of Fish and Wildlife, St. Paul, Minnesota. 27 pages.

Stein, B. A., and **S. R. Flack.** 1997. 1997 Species report card: The state of U.S. plants and animals. The Nature Conservancy, Arlington, Virginia. 26 pages.

Thompson, D. Q., R. L. Stuckey, and **E. B. Thompson.** 1987. Spread impact and control of Purple Loosestrife (*Lythrum salicaria*) in North American wetlands. U.S. Fish and Wildlife Service, Fish and Wildlife Research 2. 55 pages.

Walker, J. 1965. Vegetation changes with falling water levels in the Delta Marsh, Manitoba. Ph.D. thesis. University of Manitoba, Winnipeg, Manitoba.

White, D. J., E. Haber, and **C. Keddy.** 1993. Invasive Plants of Natural Areas in Canada. Canadian Wildlife Service, Environment Canada. Ottawa, Ontario. 121 pages.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and **E. Losos.** 1998. Quantifying threats to imperiled species in the United States. BioScience 48: 607–615.

Received 10 January 2002
Accepted 25 March 2003

Comparison of Spring Return Dates of Mountain Bluebirds, *Sialia currucoides,* and Tree Swallows, *Tachycineta bicolor* with Monthly Air Temperatures

ROBERT K. LANE[1] and MYRNA PEARMAN[2]

[1]12 Gilchrist Place, St. Albert, Alberta T8N 2M3 Canada
[2]Site 2 Comp 2 RR1, Sylvan Lake, Alberta T4S 1X6 Canada

Lane, Robert K., and Myrna Pearman. 2003. Comparison of spring return dates of Mountain Bluebirds, *Sialia currucoides,* and Tree Swallows *Tachycineta bicolor,* with monthly air temperatures. Canadian Field-Naturalist 117 (1): 110–112.

The dates of "first observed arrivals" of Mountain Bluebirds, *Sialia currucoides,* and Tree Swallows, *Tachycineta bicolor,* have been recorded for approximately 40 years near Lacombe, Alberta, Canada. Examinations of trends of these returns with average monthly temperatures for March and April, respectively, suggest trends for earlier returns and warmer temperatures, consistent with theories of climate warming.

Key Words: Mountain Bluebird, *Sialia currucoides,* Tree Swallow, *Tachycineta bicolor,* migration, climate change, air temperature, Alberta, Canada

The scientific literature contains an increasing number of references indicating that global climate change appears to be affecting some aspects of wildlife behaviour, including the timing of migration of Mountain Bluebirds, *Sialia currucoides,* and Tree Swallows, *Tachycineta bicolor*. Two examples of this work in Alberta are Sadler and Myers (1976) and Pinel et al. (1993). Useful recent summaries are found in Dunn and Winkler (1999) and Dunn et al. (2000) on the timing of nesting and egg laying, respectively.

This report compares approximately 40 years of first observed spring arrival (FOA) dates of Mountain Bluebirds and of Tree Swallows with average March and April air temperatures, respectively, recorded in the Lacombe area of central Alberta, Canada.

Records of FOA dates of Mountain Bluebirds (MOBL) and Tree Swallows (TRES) in the Lacombe

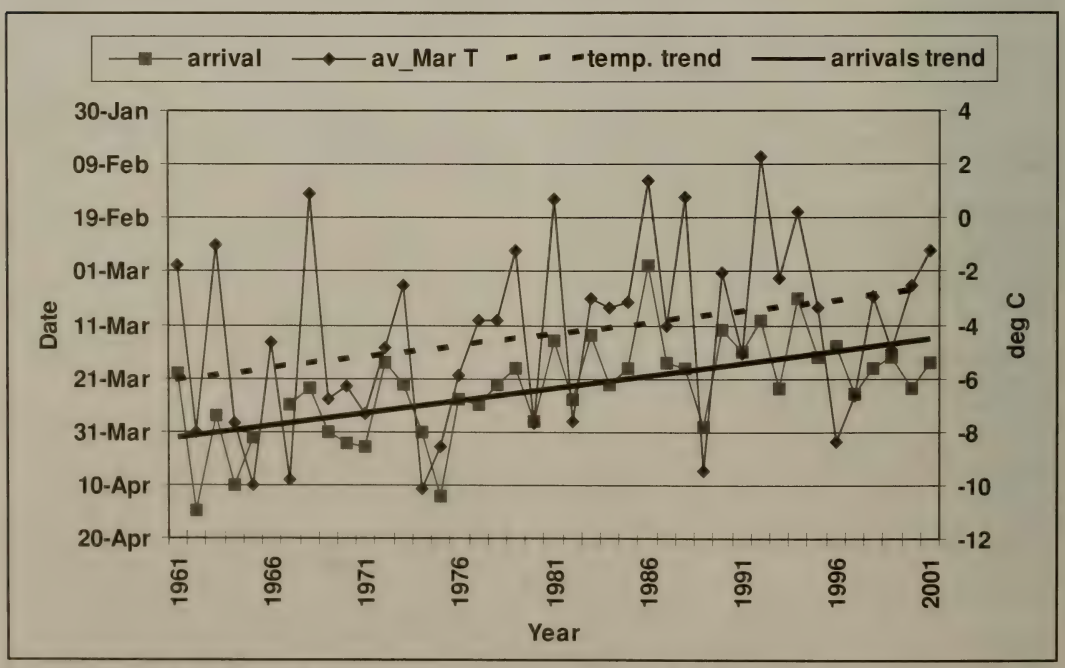


FIGURE 1. Trends of the dates of first observed arrival of Mountain Bluebirds at Ellis Bird Farm near Lacombe, Alberta, and average March temperatures.

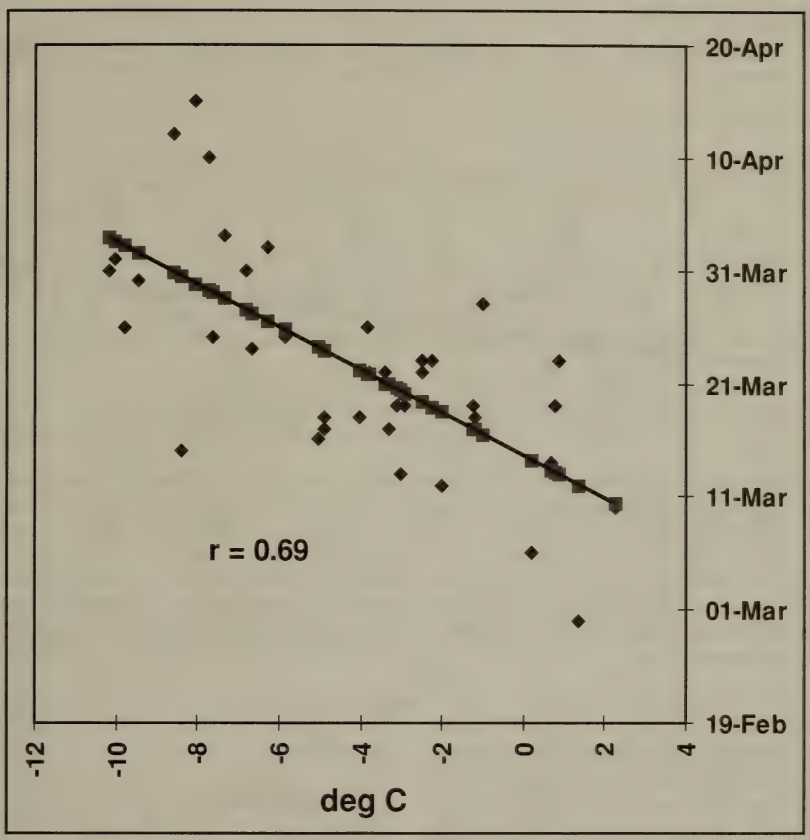


FIGURE 2. Regression analysis result for first observed arrival of Mountain Bluebirds at Ellis Bird Farm near Lacombe, Alberta, versus average March temperatures.

area were kept by Winnie Ellis of Lacombe, from 1958 (TRES) and 1961 (MOBL) until 1981. After 1981, FOA dates were recorded for both species by a biologist hired by Ellis Bird Farm Ltd., the non-profit company charged with the responsibility of carrying on the bluebird conservation efforts of Winnie and her brother, Charlie Ellis. Although FOA dates are not necessarily a true record of first spring arrival times, they do represent the last possible date that the birds returned, even if the observed arrivals did not remain in the area. There is no evidence that either species over-winters in this area. Furthermore, Charlie and Winnie Ellis and the employed biologists actively searched for MOBL each spring, as did many of the Ellis' neighbours.

Temperature data have been collected since 1907 at a federal agricultural research facility now known as the Agriculture and Agri-food Canada Lacombe Research Centre, located approximately 8 km northwest of the Ellis farm. The bird return observations are from an area of approximately 250 km^2 surrounding the Ellis farm, known as the Ellis Bird Farm Management Area (so named because it is the area in which Ellis Bird Farm Ltd. continues to operate a bluebird trail).

Trends for MOBL FOA data and average March daily temperatures for the period of record are illustrated in Figure 1. The trends show increasing average monthly temperature values and earlier observed arrival dates over the period of record. A regression plot of these data (Figure 2) produced $r = 0.69$. Using a standard baseline date of 30 January, B. Fairfield-Carter (personal communication) conducted a parametric analysis of variance for these data and found $p<0.0001$, which is significant. A similar analysis for FOA of TRES compared to average April daily temperatures is illustrated in Figure 3. In this case, a regression analysis of the data produced $r = 0.33$ and the variance analysis (B. Fairfield-Carter, personal communication) determined $p=0.1232$, which is not significant.

The trends for monthly average air temperature show increasing values; these trends are consistent with trends commonly observed in the literature. They are suggestive of global climate change. Other references to the climate trends include Folland et al. (2001) and Zhang et al. (2000). Over the 41 years that MOBL dates of arrivals have been recorded, the slope of the trend line for the average March temperature was approximately 0.09 deg./yr. and the slope

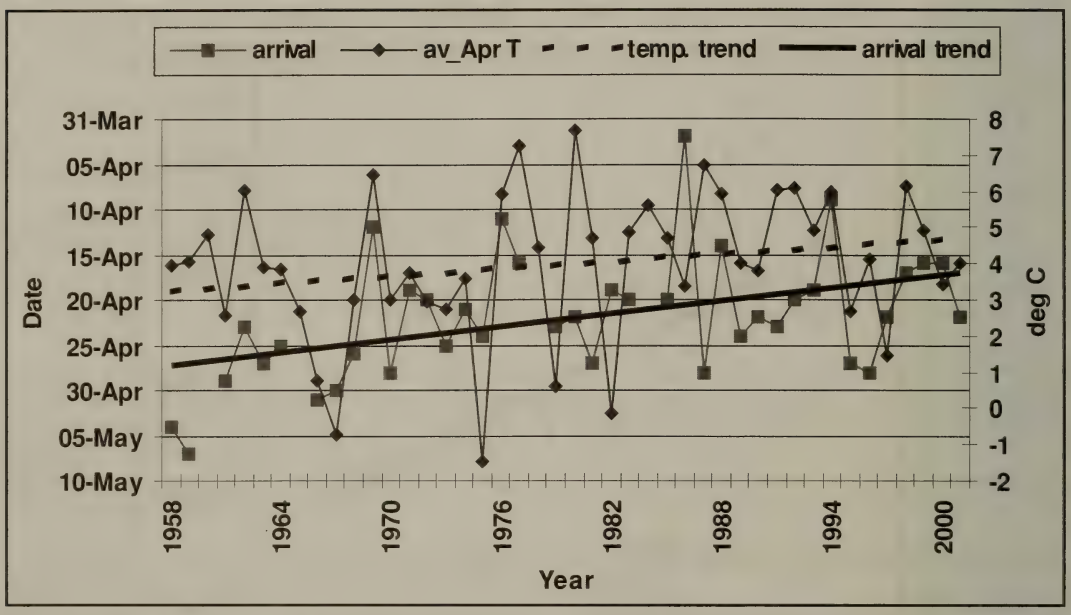


FIGURE 3. Trends of the dates of first observed arrival of Tree Swallows at Ellis Bird Farm near Lacombe, Alberta, and average April temperatures.

of the trend line for the FOA dates was approximately 0.4 days/yr. Over the 44 years that TRES dates of arrivals have been recorded, the slope of the trend line for the average April temperature was approximately 0.03 deg./yr. and the slope of the trend line for the FOA dates was approximately 0.25 days/yr. A conservative interpretation of the FOA and temperature data is that the temperature trend reflects a larger geographic trend of increasing average monthly temperatures, and that the earlier returns appear to reflect a behavioural response to this larger geographic phenomenon.

Arrival dates of MOBL and TRES on their breeding territory are influenced by many factors, including weather on their wintering grounds and along their migration routes. For this reason, local meteorological conditions might not always be the most significant factor influencing FOA dates. However, given the consistency in trends of average March temperatures, average April temperatures, and in the FOA trends of both species, this correlation warrants further examination.

Acknowledgments

We thank Winnie Ellis and Ellis Bird Farm Ltd. for supplying FOA records and also acknowledge the Meteorological Service of Canada for providing the climate data, Brenda Dale of the Canadian Wildlife Service, Environment Canada and Bob Kochtubajda of the Meteorological Service, Environment Canada for technical reviews. This research project was sponsored in part by the Red Deer River Naturalists Society through funding support from the Red Deer and District Community Foundation.

Literature cited

Dunn, P. O., and **D. W. Winkler.** 1999. Climate change has affected breeding date of tree swallows throughout North America. Proceedings of the Royal Society, London. B, 266: 2487–2490.

Dunn, P. O., K. J. Thusius, K. Kimber, and **D. W. Winkler.** 2000. Geographic and ecological variation in clutch size of tree swallows. Auk 117: 215–221.

Folland, C. K., T. R. Karl, J. R. Christy, R. A. Clarke, G. V. Gruza, J. Jouzel, M. E. Mann, J. Oerlemans, M. J. Salinger, and **S. W. Wang.** 2001. Observed climate variability and change. *In* Climate Change 2001: The Scientific Basis. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change. *Edited by* J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson. Cambridge University Press, Cambridge, United Kingdom, and New York, NY, USA. 881 pages.

Pinel, H. W., W. W. Smith and **C. R. Wershler.** 1993. Alberta Birds, 1971-1980 Volume 2 - Passerines. Natural History Occasional Paper Number 20. Provincial Museum of Alberta, Edmonton. 238 pages.

Sadler, T. S. and **M. T. Myers.** 1976. Alberta Birds 1961-1970. Natural History Occasional Paper Number 1. Provincial Museum of Alberta, Edmonton. 314 pages.

Zhang, X., L. A. Vincent, W. D. Hogg, and **A. Niitsoo.** 2000. Temperature and precipitation trends in Canada during the 20th century. Atmosphere-Ocean 38(3): 395–429.

Received 6 March 2002
Accepted 14 March 2003

Notes

Mortality of Black Bears, *Ursus americanus*, Associated with Elevated Train Trestles

KYLE R. VAN WHY and MICHAEL J. CHAMBERLAIN

School of Renewable Natural Resources, Louisiana State University Agriculture Center, Baton Rouge, Louisiana 70803 USA

Van Why, Kyle R., and Michael J. Chamberlain. 2003. Mortality of Black Bears, *Ursus americanus*, associated with elevated train trestles. Canadian Field-Naturalist 117(1): 113–115.

The Louisiana Black Bear (*Ursus americanus luteolus*), a threatened species in the United States, inhabits the Tensas and Atchafalaya River Basins of Louisiana. These basins contain three breeding populations, but dispersal among the populations is limited due to habitat fragmentation and a lack of corridors. Highways and railroads bisect the few available corridors, and mortalities occur as a result of collisions with vehicles. Waterways and flood control structures used as travel corridors by bears are crossed by road and rail bridges creating the potential for additional mortalities. We documented two mortalities associated with elevated railroad spans. Both occurred along the same span of track located within the Morganza Spillway in Pointe Coupee Parish, Louisiana, and both mortalities were a result of the bear falling from the span or being struck by a train while crossing the trestle.

Key Words: Louisiana Black Bear, *Ursus americanus luteolus*, bridges, mortality, railroads, Louisiana.

The fragmentation of habitat by roads and train tracks can isolate wildlife populations (Groot Bruinderink and Hazebroek 1996; Van Der Grift 1999). Mortality of wildlife caused by crossing of roads and railroad tracks is a common occurrence (Groot Bruinderink and Hazebroek 1996; Van der Grift 1999). For example, vehicle collisions in Florida have significantly affected both the Florida Panther (*Puma concolor coryi*) and the Florida Black Bear (*Ursus americanus floridanus*) by increasing mortality in these already sensitive populations (Wooding and Brady 1987; Foster and Humphrey 1995). Although Black Bears ranged throughout the southeast historically (Hall 1981), their range has been greatly reduced (Pelton and van Manen 1997). The Louisiana Black Bear (*U. a. luteolus*) was once widely distributed across all of Louisiana, eastern Texas, and western Mississippi (Hall 1981), but loss of habitat has considerably reduced its range. There are currently only three breeding populations of Louisiana Black Bears, all found within the Tensas and Atchafalaya River Basins (Pace et al. 2000).

Because of extensive reduction in range and considerable loss of suitable habitat, the Louisiana Black Bear was designated as federally Threatened in 1992 (Neal 1992). Furthermore, the remaining forested habitats supporting Louisiana Black Bear populations are surrounded by agricultural land, with very few corridors connecting woodland tracts (Black Bear Restoration Committee 1997). The few available corridors are bisected by a series of road and rail systems. Interstates [highways] 190 and 10 separate the two southern populations (Pace et al. 2000), and Interstate 20 bisects the third population (Marchinton 1995; Anderson 1997).

The most common cause of mortality for Louisiana Black Bears during 1992-2000 was vehicular collisions (Pace et al. 2000). Although wildlife deaths associated with trains are well documented (Van der Grift 1999), we describe two Black Bear deaths associated with elevated train trestles, a finding not detailed in the literature. The location of these mortalities occurred along a section of track bisecting the Morganza Spillway, located in Pointe Coupee Parish, Louisiana. The Morganza Spillway is located within the central Atchafalaya River Basin, which supports one of the three remaining Louisiana Black Bear populations.

Methods

Capture of Black Bears in Louisiana has occurred in all three populations (Wagner 1995; Weaver 1999). Those in the Tensas River Basin have been trapped and monitored from 1988 to the present (D. Anderson, USFWS, personal communication). Those in the Atchafalaya River Basin were monitored during the late 1960s after initial reintroduction efforts occurred (Taylor 1971) and again during the 1990s, with much of the research focused within the Morganza Spillway (Wagner 1995). Bears captured

after 1988 were marked with colored and numbered ear tags, in addition to being tattooed with an identification number. A select number of captured bears have been fitted with radio-collars within the three populations and monitored by both ground and aerial telemetry (Wagner 1995; Weaver 1999). Because of the threatened status of the Louisiana Black Bear, state and federal wildlife personnel often document sightings and reports of bears throughout the state. All documented Black Bear mortalities are investigated to determine cause of death and to collect vital life history information if possible (Pace et al. 2000).

We discovered two separate mortality events in Louisiana associated with elevated railroad spans. Each mortality event was spatially referenced using a Global Positioning System (GPS), as was each site where bears were captured. We subsequently examined spatial relationships between both mortality events and locations where each bear was captured.

Results

Two Louisiana Black Bears were found below an elevated span of railroad trestle. Injuries associated with the remains of both bears showed blunt force trauma and suggested that they either had fallen from the tracks or had been struck by a train while attempting to cross the span. Both incidents occurred on the same elevated section of track, which crosses the Morganza Spillway in Pointe Coupee Parish, Louisiana. The elevated span is approximately 1900 m in length, and distance between the positions where the two bears were recovered was 1490 m, indicating that bears were at opposite ends of the elevated span.

The first bear, an adult female, was discovered on 14 September 1999 beneath the elevated span crossing Johnson Bayou (UTM 622833.94, 3395496.69). She had been captured twice during 1992–1993, and both capture locations were within 3500 m of where she was recovered. The closest distance between the recovery site and the point where the trestle became elevated was approximately 100 m. The second bear, an adult male, was found along the same span of track (UTM 623913.66, 3394470.19). This bear was discovered on 31 July 2001 and had been captured on 28 July 1996, approximately 9881 m from where he was recovered. The closest distance between the recovery site and the point where the trestle became elevated was approximately 300 m.

Discussion

Based on capture and recovery information, it seems plausible that both bears maintained home ranges close to, or overlapping, the elevated train trestle. Indeed, large carnivores may use train tracks and rights-of-way as travel corridors in fragmented habitats (Van der Grift 1999). In the southeast much of the available woodland habitat is fragmented (Wooding et al. 1994) and connected by only narrow woodland corridors (Pelton 1990). The use of rights-of-way as corridors would promote bear movement between isolated woodland patches where Black Bears are found. Anderson (1997) found that movements between isolated forest patches via natural corridors were relatively common for Black Bears. Specifically, corridors used were usually those with low human activity levels; they ranged in size from 5 m to 73 m along waterways (Anderson 1997). Similarly, Clevenger and Waltho (2000) found that carnivores were more likely to use crossings associated with relatively low human activity levels.

Railroad bridges may be used by wildlife for crossing larger waterways or lowland areas. In many areas railroad bridges often have little human activity associated with them (besides the passing of the trains), and many tracks and bridges are no longer in use. Our findings suggest that Black Bears may feel secure traveling elevated trestles relative to crossing waterways or lowland areas with low cover.

Van der Grift (1999) reviewed literature relating to wildlife use of railroads, but little is still known about the use of railroad tracks and rights-of-way by wildlife. He describes one incident involving Moose (*Alces alces*) trapped and killed on elevated trestles when their legs fell between the ties while trying to escape approaching trains (Van der Grift 1999). In addition to the two mortalities we describe, a bear was witnessed being struck by a train in Arkansas on an elevated span in 2000. This bear was struck while crossing an elevated span with one cub (Goad 2001).

It is unknown at what rate this type of activity occurs and what impact it may have on Black Bear population status. The use of bridges as corridors and travel lanes may aid in dispersal of bears from isolated populations, but mortality associated with accidents may negatively affect population viability. For already endangered or threatened species such as the Louisiana Black Bear, even a few mortalities can have severe implications on already stressed populations (Van der Grift 1999). Documenting accidents along roads and railway trestles may help identify preferred corridors and dispersal patterns of Black Bears in regions with isolated populations and fragmented habitats.

Acknowledgments

We thank D. LeBlanc and M. Davidson for help obtaining reports of bear mortalities. R. Eastridge added information regarding bear management in Arkansas, and D. Anderson and R. Wagner contributed valuable information on Louisiana Black Bear research. We also thank the biologists, agents, managers, and other individuals who reported bear mortalities and assisted with data collection.

Literature Cited

Anderson, D. R. 1997. Corridor use, feeding ecology, and habitat relationships of Black bears in a fragmented landscape in Louisiana. M.S. thesis, University of Tennessee, Knoxville, Tennessee. 123 pages.

Black Bear Restoration Committee. 1997. Black Bear Restoration Plan, Baton Rouge, Louisiana. 126 pages.

Clevenger, A. P., and **N. Waltho.** 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. Conservation Biology 14: 47–56.

Foster, M. L., and **S. R. Humphrey.** 1995. Use of highway underpasses by Florida panthers and other wildlife. Wildlife Society Bulletin 23: 95–100.

Goad, D. 2001. Train and bear collide. International Bear News 10: 30.

Groot Bruinderink, G. W. T. A., and **E. Hazebroek.** 1996. Ungulate traffic collisions in Europe. Conservation Biology 10: 1059–1067.

Hall, E. R. 1981. The mammals of North America. John Wiley and Sons, New York, New York. 1181 pages.

Marchinton, F. B. 1995. Movement ecology of Black bears in fragmented bottomland hardwood habitat in Louisiana. M.S. thesis, University of Tennessee, Knoxville, Tennessee. 107 pages.

Neal, W. M. 1992. Threatened status for Louisiana Black bear. Federal Register 55: 25341–25345.

Pace, R. M. III, D. R. Anderson, and **S. Shively.** 2000. Sources and patterns of mortality in Louisiana Black bears. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 54: 365–373.

Pelton, M. R. 1990. Black bears in the southeast: to list or not to list. Eastern Workshop on Black Bear Research and Management 10: 155–161.

Pelton, M. R., and **F. T. van Manen.** 1997. Status of Black bears in the southeastern United States. Pages 31-44 *in* Proceedings of the Second International Symposium on the Trade of Bear Parts. *Edited by* A. L. Gaski and D. F. Williamson. TRAFFIC USA - World Wildlife Fund, Washington, D.C. 239 pages.

Taylor, D. F. 1971. A radio-telemetry study of the Black bear (*Euarctos americanus*) with notes on its history and present status in Louisiana. M.S. Thesis, Louisiana State University, Baton Rouge, Louisiana. 87 pages.

Van der Grift, E. A. 1999. Mammals and railroads: impacts and management implications. Lutra 42: 77–98.

Wagner, R. O. 1995. Movement patterns of Black bears in south central Louisiana. M.S. Thesis, Louisiana State University, Baton Rouge, Louisiana. 56 pages.

Weaver, K. M. 1999. The ecology and management of Black bears in the Tensas River Basin of Louisiana. Ph.D. dissertation, University of Tennessee, Knoxville, Tennessee. 280 pages.

Wooding, J. B., and **J. R. Brady.** 1987. Black bear roadkills in Florida. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 41: 438–442.

Wooding, J. B., J. A. Cox, and **M. R. Pelton.** 1994. Distribution of Black bears in the southeastern coastal plain. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 48: 270–275.

Received 4 October 2001
Accepted 24 February 2003

Incidence of Mink, *Mustela vison*, and River Otter, *Lutra canadensis*, in a Highly Urbanized Area

L. DAVID MECH[1]

Biological Resources Division, U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 – 37th St. S.E., Jamestown, North Dakota 58401-7317 USA
[1]Mailing address: The Raptor Center, 1920 Fitch Avenue, University of Minnesota, St. Paul, Minnesota 55108 USA

Mech, L. David. 2003. Incidence of Mink, *Mustela vison*, and River Otter, *Lutra canadensis*, in a highly urbanized area. Canadian Field Naturalist 117(1): 115–116.

Mink (*Mustela vison*) frequently inhabited or traversed a residential, business, and industrial part of the Twin Cities, Minnesota, with little water or natural vegetation. At least one River Otter (*Lutra canadensis*) also resided on a small pond on a golf course in the area for several winter months.

Key Words: Mink, *Mustela vison*, River Otter, *Lutra canadensis*, urban wildlife, Minnesota

Urban wildlife, including carnivores and raptors, is common. Where large marshes or other extensive waterways exist in cities and suburbs, Muskrats (*Ondatra zibethicus*), Mink (*Mustela vison*), and even Beavers (*Castor canadensis*) and River Otters (*Lutra canadensis*) can be expected. Such areas are really islands of suitable habitat in seas of urbanization. However, this note documents Mink and an otter inhabiting an urban area without such natural habitat.

The study area is a region 3 km^2 located in Lauderdale, Minnesota (Ramsey County), along the border between the cities of St. Paul and Minneapolis. It has long been a heavily populated residential, industrial, and business area interlaced with paved streets, highways, and parking lots, and a

TABLE 1. Records of Mink in residential, industrial, and business area of Lauderdale, Minnesota.

Date	Location	Distance from nearest natural habitat
10 September 1996	State Highway 280 and Larpenteur Avenue[1]	5.7 km
24 October 1999	State Highway 280 and Broadway Avenue[1]	5.0 km
6 November 1999	Interstate highway 36 and Cleveland Avenue[1]	3.3 km
6-30 November 2000	1.1-ha Walsh Lake (golf course pond)[2]	4.9 km

[1]Road-killed.
[2]Tracks in snow.

golf course. The only nearby natural vegetation is an embankment up to 15 m wide along each side of a railroad track. The only water is a pond of 1.1 ha (Walsh Lake) surrounded by a golf course and residential yards. A storm sewer feeds the pond. The nearest natural Mink habitat is 3.3-5.7 km away, with houses, yards, businesses, and six to eight lanes of interstate highway intervening. The nearest extensive waterways where otters might be expected are 3.5-6.0 km away, also separated from the area by the same type of surroundings.

Over a period of 4 years, I found three road-killed Mink in this area and tracks in the snow of a Mink frequenting the golf course pond (Table 1). The dead Mink were 0.25, 1.00, and 1.50 km from the pond. The otter used the pond from at least 26 December 2002 through 11 April 2003 based on extensive tracks, slides, and feeding holes through thin ice. There was neither natural vegetation nor waterway between the pond and the dead Mink. Wherever the Mink and otter came from, they had to have passed through yards, lawns, streets, highways, and parking lots, ditches, or possibly sewers.

The pond, which has a shoreline of about 375 m, was much smaller than areas usually reported to be inhabited by Mink or otters. In North America, reported mean linear home ranges for Mink varied from 5 250 to 7 519 m (Whitman 1981; Stevens et al. 1997). Average home range sizes ranged from 282 to 1 141 hectares (Arnold and Fritzell 1987; Eagle 1989). Thus the pond probably constituted only a small part of one Mink's home range, despite the fact that there was no vegetation or waterway connecting it with any other natural Mink habitat. Otters roam over areas 8-78 km in extent (Melquist and Hornocker 1983).

These findings document the ubiquity and great adaptability of Mink and otters.

Acknowledgments

This study was supported by the biological Resources Division of U.S. Geological Survey and the U.S. Department of Agriculture, North Central Research Station.

Literature Cited

Arnold, T. W., and **E. K. Fritzell.** 1987. Activity patterns, movements, and home ranges of prairie mink. Prairie Naturalist 19: 25–32.

Eagle, T. C. 1989. Movement patterns of mink in the prairie pothole region of North Dakota. Ph.D. thesis, University of Minnesota, St. Paul. 143 pages.

Melquist, W. E., and **M. G. Hornocker**. 1983. Ecology of river otters in west-central Idaho. Wildlife Monographs 83. 60 pages.

Stevens, R. T., T. L. Ashwood, and **J. M. Sleeman**. 1997. Fall-early winter home ranges, movements, and den use of male mink, *Mustela vison* in eastern Tennessee. Canadian Field-Naturalist 111: 312–314.

Whitman, J. S. 1981. Ecology of the mink (*Mustela vison*) in west-central Idaho. M.S. thesis. University of Idaho, Moscow, Idaho. 101 pages.

Received 8 January 2001
Accepted 22 May 2003

An *in situ* Observation of Webover Hunting by the Giant Pacific Octopus, *Enteroctopus dofleini* (Wülker, 1910)

JAMES A. COSGROVE

Royal British Columbia Museum, 675 Belleville Street, Victoria, British Columbia, V8W 9W2 Canada
e-mail: jcosgrove@royalbcmuseum.bc.ca

Cosgrove, James A. 2003. An in situ observation of webover hunting by the Giant Pacific Octopus, *Enteroctopus dofleini* (Wülker, 1910). Canadian Field-Naturalist 117(1): 117–118.

Five scuba divers observed a female Giant Pacific Octopus, *Enteroctopus dofleini* (Wülker, 1910) using the webover technique of speculative hunting.

Key Words: Mollusca, Cephalopoda, Giant Pacific Octopus, *Enteroctopus dofleini*, hunting, webover, British Columbia.

It has been reported that cephalopods have seven modes of hunting: ambushing, luring, stalking, pursuing, speculative hunting, hunting in disguise, and cooperative hunting (Hanlon and Messenger 1996). Speculative hunting has been described as a pounce (on an object such as kelp, a coral head or a rock) with outspread web and then a feel around under the web for the presence of food items (Yarnall 1969). This type of hunting has also been reported for *Octopus_briareus* (Hochberg and Couch 1971; Hanlon and Wolterding 1989), *Octopus cyanea* (Yarnall 1969; Forsythe and Hanlon 1997), *Octopus vulgaris* (Mather 1991), and *Octopus bimaculatus* (R. F. Ambrose, personal communication *in* Hanlon and Messenger 1996).

Little has been reported about the hunting techniques of *Enteroctopus dofleini* (Wülker, 1910), possibly because of the cold water it lives in or the water's poor visibility. Most available information on its feeding is based on the remains of hard-bodied prey found in the midden heap (Hartwick et al. 1981; Hartwick 1983; Robinson and Hartwick 1986; Cosgrove 1987; Vincent et al. 1998; Dodge and Scheel 1999). Some information has come from the stomach contents of harvested *E. dofleini* (Mottet 1975). Mather et al. (1985) conducted field studies using sonic tags to demonstrate the frequency and duration of hunting trips of *E. dofleini.*

Enteroctopus dofleini hunts mostly by speculation using the tips of the arms to probe around and under rocks (personal observation). In most cases the prey is either captured by the suckers or flushed out, after which the pursuit mode of hunting is employed. When prey is discovered in the open the pursuit mode is also employed.

Anderson (1991) reported aquarium observations of *E. dofleini* capturing and eating apparently healthy fish. Johnson (1942) noted that *Enteroctopus dofleini* would ambush by "suddenly striking out at prey with a tentacle and grasping it with the aid of the suckers", and he noted that the octopus was ineffective using this method while ambushing shrimp and small fishes that lived among seaweeds. Johnson also described an attempt to catch larger numbers of small prey "by throwing over them a web formed by the loose extensible membrane of skin connecting the base of the tentacles." Johnson viewed this hunting mode from a rowboat looking down into the water near the Friday Harbor Laboratories of the University of Washington. Mather (1991, 1998) coined the term "webover" to describe this hunting mode. This webover hunting method is described here in greater detail.

On 14 February 1999 five scuba divers encountered a female *Enteroctopus dofleini* at a depth of 11.6 metres among some rocks in the Ogden Point Breakwater (48° 24.9′ N, 123° 23.2′ W) near Victoria, British Columbia, Canada. The female had an estimated weight of 10 – 12 kg and an arm span of approximately 2 metres. The female completely ignored the divers. The octopus selected boulders approximately two-thirds of a metre in diameter and moved with some speed from one boulder to the next. As she approached each boulder she would flare her web over the boulder and settle onto the top of the boulder with her arms and interbrachial web completely enclosing the rock. As she enclosed the rock, the arms and interbrachial web became white. The mantle remained red except for two large mantle white spots on the dorsal surface. The white spots changed from red to white and then returned to red in less than 2 seconds. The arms and web returned to red within 10 to 20 seconds of the female settling on the rock. As the arms and web enveloped the rock small fishes escaped from underneath. The tips of the octopus's arms could be seen moving in the spaces underneath the boulder. Over a period of approximately 10 minutes a series of six or seven pounces were observed each following the identical pattern. This timing of pounces appears to agree with the observations of Johnson (1942), who reported 15 pounces in a 20-minute period. At no time was the octopus seen to capture a fish.

In an attempt to determine if the octopus was actually hunting, a diver brought a small crab (*Oregonia gracilis* Dana 1851) in contact with the suckers on one

of the octopus arms as it probed under the rock. The crab was quickly taken and moved under the web. The arm returned and contacted a second offered *O. gracilis* and that was also quickly taken, as was a third crab (*Chorilia longipes* Dana 1851) offered to a different arm. Whether or not the crabs were moved to the mouth was not observed. Octopuses can hold crabs for future consumption (Hanlon and Messenger 1996). At this time the octopus settled in a hollow under a boulder. The reddish colour changed to a mottled light brown and stayed that way for several minutes. Eventually the female moved under a nearby rock still holding the crabs in her web and maintained the mottled colour. Observations ended after about 20 minutes. In the process of moving from boulder to boulder the octopus had traveled from a depth of 11.6 metres to a depth of less than 10 metres. This supports the opinion that the female was not feeling threatened by the divers, as a threatened *E. dofleini* will normally move under cover or will flee to deeper water (personal observation).

The spaces under the boulders contained a number of smaller fishes including juvenile *Sebastes caurinus* (Richardson 1845) (Copper Rockfish), juvenile *Sebastes emphaeus* (Starks 1911) (Puget Sound Rockfish), *Oxylebius pictus* (Gill 1862) (Painted Greenling) and various small sculpins. At no time did the octopus attempt to pursue or capture any of the fishes that were nearby or in the open once she had flushed them. The octopus also showed no interest in the numerous small crabs that were also available until they were brought in contact with her suckers. In general these small crabs, including the ones she accepted, would not normally have been food for an octopus of this size (personal observation).

Acknowledgments

My thanks to Jeannie Cosgrove, Bill Nadeau, Billy Shaw, and Ivo Van Bastelaere for sharing the dive and their observations with me. Thanks also to Roland Anderson and Phil Lambert for reviewing several drafts of this paper.

Literature Cited

Anderson, R. C. 1991. The fish catching ability of *Octopus dofleini*. Journal of Cephalopod Biology 2: 75–76.

Cosgrove, J. A. 1987. Aspects of the natural history of *Octopus dofleini*, the Giant Pacific Octopus. M.Sc. thesis, University of Victoria. Victoria, British Columbia 100 pages.

Dodge, R., and **D. Scheel.** 1999. Remains of the prey – recognizing the midden piles of *Octopus dofleini* (Wülker). The Veliger 42: 260–266.

Forsythe, J. W., and **R. T. Hanlon.** 1997. Foraging and associated behavior by *Octopus cyanea* Gray, 1849 on a coral atoll, French Polynesia. Journal of Experimental Marine Biology and Ecology 209: 15–39.

Hanlon, R. T., and **J. B. Messenger.** 1996. Cephalopod Behaviour. Academic Press, London. 232 pages.

Hanlon, R. T., and **M. R. Wolterding.** 1989. Behavior, body patterning, growth and life history of *Octopus briareus* cultured in the laboratory. American Malacological Bulletin 7: 21–45.

Hartwick, E. B. 1983. *Octopus dofleini*. Pages 277-291 *in* Cephalopod Life Cycles, Volume 1. *Edited by* P. R. Boyle. Academic Press, London.

Hartwick, E. B., L. Tulloch, and **S. MacDonald.** 1981. Feeding and growth of *Octopus dofleini*. The Veliger 24: 129–138.

Hochberg, F. G., and **J. A. Couch.** 1971. Biology of cephalopods. Pages V1221-V1228 *in* Tektite II, Scientists in the Sea, Mission 8-50. United States Department of the Interior, Washington, D.C.

Johnson, M. W. 1942. Some observations of the feeding habits of the octopus. Science 95 (2471): 478–479.

Mather, J. A. 1991. Foraging, feeding, and prey remains in middens of juvenile *Octopus vulgaris* (Mollusca: Cephalopoda). Journal of Zoology (London) 224: 27–39.

Mather, J. A. 1998. How do octopuses use their arms? Journal of Comparative Psychology 112(3): 306–316.

Mather, J. A., S. Resler, and **J. A. Cosgrove.** 1985. Activity and movement patterns of *Octopus dofleini*. Marine Behavior and Physiology 11: 301–314.

Mottet, M. G. 1975. The fishery biology of *Octopus dofleini* (Wülker). Management and Research Division, Washington, Department of Fisheries Technical Report (16). 37 pages.

Robinson, S. M. C., and **E. B. Hartwick.** 1986. Analysis of growth based on tag-recapture of Giant Pacific octopus *Octopus dofleini martini*. Journal of Zoology (London) 209: 559–572.

Vincent, T. L. S., D. Scheel, and **K. R. Hough.** 1998. Some aspects of diet and foraging behavior of *Octopus dofleini* (Wülker, 1910) in its northwest range. Marine Ecology 19: 13–29.

Yarnall, J. L. 1969. Aspects of the behaviour of *Octopus cyanea* Gray. Animal Behaviour 17: 747–754.

Received 11 December 2000
Accepted 16 May 2003

Heavy Metal Concentrations in Arctic Foxes, *Alopex lagopus*, in the Prudhoe Bay Oil Field, Alaska

WARREN B. BALLARD[1,2], MATTHEW A. CRONIN[1,3], MARTIN D. ROBARDS[1], and WILLIAM A. STUBBLEFIELD[4]

[1]LGL Alaska Research Associates, Inc., 4175 Tudor Centre Drive, Suite 202, Anchorage, Alaska 99508 USA
[2]Department of Range, Wildlife, and Fisheries Management, Texas Tech University, Box 42125, Lubbock, Texas 79804 USA
[3]School of Natural Resources and Agricultural Science, University of Alaska, Fairbanks, Alaska 99775 USA
[4]ENSR Toxicology Laboratory, 4303 W. LaPorte Avenue, Fort Collins, Colorado 85021 USA

Ballard, Warren B., Matthew A. Cronin, Martin D. Robards, and William A. Stubblefield. 2003. Heavy metal concentrations in Arctic Foxes, *Alopex lagopus*, in the Prudhoe Bay Oil Field, Alaska. Canadian Field-Naturalist 117(1): 119–121.

Liver and kidney tissue samples from 30 Arctic Foxes (*Alopex lagopus*) collected in the Prudhoe Bay Oil field in Alaska during 1994 were analyzed for barium, cadmium, chromium, mercury, nickel, selenium, and vanadium. Mean concentrations for all metals were higher in kidney than liver tissues. Mean liver concentrations (μg/g dry weight) for females and male foxes, respectively, were 0.12 and 0.09 for barium, 0.48 and 0.57 for cadmium, 1.03 and 1.04 for chromium, 1.10 and 0.54 for mercury, 0.17 and undetectable for nickel, 3.00 and 2.69 for selenium, and 0.05 and 0.06 for vanadium. Heavy metal concentrations in Arctic Fox liver and kidney tissues were low compared to non-industrial areas in Canada and the Norwegian Arctic. Arctic foxes in the Prudhoe Bay oil field have relatively low concentrations of heavy metals, although most (25 of 30) of the foxes analyzed were juveniles and concentrations may differ in adults.

Key Words: Arctic Fox, *Alopex lagopus,* barium, cadmium, chromium, mercury, nickel, oil, selenium, vanadium, Prudhoe Bay, Alaska.

Handling and disposal of oil drilling wastes and other industrial materials on Alaska's North Slope were predicted to expose tundra biota to heavy metals, salts, and hydrocarbons (U. S. Department of the Interior 1972*). Stubblefield et al. (1992*) examined the potential for lower trophic levels to accumulate metals associated with North Slope drilling wastes. They indicated that with the possible exception of certain metals in phytoplankton, there was no indication that drilling operation-related materials bioaccumulated in tundra biota. However, their study did not evaluate bioaccumulation in predators. The purpose of this study was to analyze a sample of Arctic Fox (*Alopex lagopus*) tissues for heavy metal concentrations within the Prudhoe Bay oil field, Alaska, and compare our results with those from other areas.

Methods

The study was conducted in the Prudhoe Bay oil field and included the Prudhoe Bay Unit (within 147°50′ – 149°10′N longitude and 70°25′–70°10′W latitude). The area has been described by Pollard et al. (1996). The PBU is a system of oil production facilities and supporting infrastructure including 44 producing wells, 19 non-producing wells, 7 gathering centers, 2 gravel landing strips for jet aircraft, and 2 base camps for workers. All facilities are supported by gravel pads and are connected by a network of primary and secondary (access) gravel roads totaling 278 km in length.

During January and February 1994 Arctic Foxes were live trapped with Havahart®, traps and then shot. Foxes were collected as part of a program to reduce rabies exposure to oil slope workers. Ninety-nine foxes were trapped, of which 30 were analyzed for heavy metals.

Metals to be analyzed were selected based upon their extent of use in drilling operations and their bioaccumulative potential (W. Stubblefield, unpublished data). These included mercury (Hg), selenium (Se), barium (Ba), cadmium (Cd), chromium (Cr), nickel (Ni), and vanadium (Vd). Of these metals, mercury and selenium, generally in the organo-metal form, are known to bioaccumulate; the other metals have not been reported to accumulate significantly in the tissues of consumers (ENSR Consulting and Engineering, and Environmental Science and Engineering, Inc. 1992*).

Chemical analyses were performed by Columbia Analytical Services, Inc. (Kelso, Washington, USA). The Mass Spectrum test (method 200.8, U. S. Environmental Protection Agency [EPA] 1991*) was used since this method offers lower detection limits than Optical Emission Spectrum analyses. Environmental Protection Agency methods 7471 and 7740 (EPA 1991*) were used for mercury and selenium, respectively. Prior to analyses all tissues were exposed to gamma radiation to reduce exposure to rabies virus.

Analytic data were grouped by element, and analyzed using a two-tail Student's t-test (Snedecor and Cochran 1980) with $P \leq 0.05$ required for significance.

Evaluation of tissue metal concentrations indicated that many nickel (26 of 30) and vanadium (17 of 30) liver and kidney concentrations were below the

analytical detection limit. Detection levels for metal concentrations given as µg/g dry weight were as follows: barium - 0.05, cadmium - 0.02, chromium - 0.2, mercury - 0.05, nickel - 0.2, selenium - 1.0, and vanadium - 0.05. Actual tissue concentrations for non-detectable values lay somewhere between the method detection limit and zero. To estimate both means and variances for all fox chemistry data, including non-detectable data, Helsel's (1990) Robust Method was used with software by Newman et al. (1995). This approach uses regression values above the detection limit for a particular analyte to predict values below the detection limit.

Results and Discussion

There were no differences ($P > 0.05$) in metal concentrations by age or sex, except that mean kidney mercury concentrations were higher ($P < 0.05$) in female than male Arctic Foxes. Consequently metal concentrations by sex and age were pooled. Mean liver concentrations (mg/g dry weight) for female and male foxes, respectively, were 0.12 and 0.09 for barium, 0.48 and 0.57 for cadmium, 1.03 and 1.04 for chromium, 1.10 and 0.54 for mercury, 0.17 and not calculable for nickel, 3.00 and 2.69 for selenium, and 0.05 and 0.06 for vanadium (Table 1). Cadmium, mercury, and selenium concentrations in kidney tissues were higher ($P \leq 0.05$) than those found in liver tissues.

Published data on metal concentrations of Arctic Fox kidney and liver are limited except from a relatively "contaminant-free" area in Svalbard, Norway (Prestrud et al. 1994). Analytes common to both studies included cadmium, mercury, and selenium for liver and cadmium for kidney. Prestrud et al. (1994) presented their data as wet weight concentrations (wwt) so we also report wet weight concentrations for cadmium, mercury, and selenium.

Prestrud et al. (1994) found no differences ($P > 0.10$) in heavy metal concentrations between sexes for any of the metals analyzed in liver and kidney tissues, but did find that adult (>1-year old) foxes had higher concentrations of cadmium in both tissues than foxes <1-year old. Mean wet weight cadmium (0.53 ± 0.50) and selenium (2.7 ± 2.5) concentrations in liver tissues were higher ($P \leq 0.05$) from Svalbard male and female Arctic Foxes than those from Prudhoe Bay, Alaska (0.16 ± 0.14 and 0.87 ± 0.28, respectively). Mean liver mercury concentrations were also higher in Norwegian foxes (0.37 ± 0.43) than those from Prudhoe Bay (0.25 ± 0.28), but this difference was not significant ($P > 0.05$). Mean kidney cadmium concentrations were also higher ($P \leq 0.05$) in Svalbard foxes than in male or female foxes from Prudhoe Bay, Alaska.

Smith and Armstrong (1975) reported mercury levels in terrestrial carnivores from the Holman area, Northwest Territories, Canada and found that mercury levels (0.76 ± 1.12 mg/g wwt) in foxes were higher than those found in Caribou (*Rangifer tarandus*) or Wolves (*Canis lupus*) from the same area. Arctic Fox liver mercury concentrations were higher ($P \leq 0.05$) than those from Prudhoe Bay, Alaska.

Svalbard Polar Bears (*Ursus maritimus*) were found to have mercury, cadmium, and selenium concentrations similar to those in Arctic Foxes from the same area (Prestrud et al. 1994). As with Svalbard foxes, Polar Bears had higher levels of these metals in livers than foxes from Prudhoe Bay, Alaska (Prestrud et al. 1994). Canadian Arctic (Norstrom et al. 1986) and Greenland (Dietz et al. 1995) Polar Bears had liver mercury concentrations (wwt) ranging from 20 to 70 µg/g and 1.35 to 24.8 µg/g, respectively, both of which were higher than concentrations from either Svalbard or Alaskan Arctic Foxes. This result may be because Polar Bears feed

TABLE 1. Mean (±SD) concentrations (mg/g dry weight) of heavy metals contained in Arctic Fox liver and kidney tissues (14 females and 16 males) from the Prudhoe Bay oil field, Alaska during January and February 1994.

	Liver		Kidney	
Analyte	**Female**	**Male**	**Female**	**Male**
Barium[1]	0.120 (±0.165)	0.089 (±0.078)	0.102 (±0.043)	0.135 (±0.055)
Cadmium	0.476 (±0.517)	0.568 (±0.386)	1.533 (±0.951)	1.998 (±1.137)
Chromium	1.029 (±0.276)	1.038 (±0.344)	1.021 (±0.208)	0.963 (±0.243)
Mercury[3]	1.098 (±0.871)	0.539 (±0.781)	2.480 (±1.410)[3]	1.228 (±1.126)[3]
Nickel[1]	0.173 (±0.239)	NC[2]	0.235 (±0.132)	NC[2]
Selenium	3.000 (±1.038)	2.688 (±0.831)	4.357 (±1.008)	4.000 (±0.791)
Vanadium[1]	0.053 (±0.058)	0.057 (±0.058)	0.061 (±0.029)	0.079 (±0.025)

[1]Not all values were measurable (i.e., non-detectable). Mean and standard deviation estimated using Helsel's Robust Method (Helsel 1990).
[2]NC: Not calculable, insufficient measured values to permit calculation of mean and variance in samples.
[3]Results significantly different between sexes in kidney samples ($P < 0.05$).

on seals (*Phoca hispida, Erignathus barbatus, Phoca groenlandica*, and *Cystophora cristata* [Kolenosky 1987]) which are typically high in heavy metal concentrations (Dietz et al. 1995).

Prestrud et al. (1994) concluded that observed concentrations of metals in Arctic Fox tissues in Norway were at levels which did not suggest significant anthropogenic contamination. They suggested that the cadmium and mercury concentrations they observed in Norwegian Arctic Foxes would not be expected to cause toxicological effects. Because lower concentrations of tissue metals were found in Arctic Foxes in the Prudhoe Bay area we would expect their conclusions to apply to our study area as well.

Arctic Foxes in Prudhoe Bay, Alaska may rely more on food discarded by humans (Ballard et al. 2000) than Norwegian foxes. This could result in less bioaccumulation of heavy metals from human food than natural food sources. Prudhoe Bay Arctic Foxes, because of a more stable anthropogenic food source (Ballard et al. 2000), may remain inland during winter instead of scavenging on Polar Bear kills on sea ice. Also, long-range transport of atmospheric pollutants and natural sources of pollutants may contribute to the higher heavy metal concentrations found in Norwegian foxes. Our results suggest there has been no significant uptake of heavy metals by juvenile Arctic Foxes associated with oil drilling in Prudhoe Bay, Alaska. However, 83% of our sample (25 of 30 foxes) was composed of juvenile foxes which may not have been alive long enough to accumulate higher levels of heavy metals. A larger sample of adult foxes should be tested.

Acknowledgments

This study was funded by BP Exploration (Alaska) Inc. with additional funding by ARCO Alaska, Inc. We thank Michelle Guilders for coordination of the project. We also thank E. Follmann, D. Ritter, E. Arnold, L. E. Noel, and B. J. Pierson for technical and analytical support. We also thank Jeff Selinger, Kirk Waggoner, and personnel from BPXA and ARCO Environmental and Security Department for their assistance in the field. This is Texas Tech University College of Agricultural Sciences and Natural Resources technical publication T-9-844.

Documents Cited [marked * in text citations]

ENSR Consulting and Engineering, and Environmental Science and Engineering, Inc. 1992. Final report bioaccumulation of heavy metals, salts, and hydrocarbons in lower-trophic levels in the Prudhoe Bay and Kuparuk fields, 1988. Final report: 6090-003. Prepared by ENSR Consulting and Engineering, Fort Collins, Colorado, for BP Exploration (Alaska) Inc., Anchorage, Alaska, USA. 135 pages + appendices.

Rodrigues, R., R. O. Skoog, and **R. H. Pollard.** 1994. Inventory of arctic fox dens in the Prudhoe Bay oil field, Alaska. 1993 Final Report. Prepared for BP Exploration (Alaska) Inc. by LGL Alaska Research Associates, Inc., Anchorage, Alaska. 37 pages.

United States Department of the Interior. 1972. Final Environmental Impact Statement, Proposed Trans-Alaska Pipeline. Volume 4. Evaluation of environmental impact. Anchorage, Alaska.

United States Environmental Protection Agency. 1991. Methods for the determination of metals in environmental samples. Office of Research and Development, Washington, D.C., EPA/600/4-91/010, 293 pages.

Literature Cited

Ballard, W. B., M. A. Cronin, R. Rodrigues, R. O. Skoog, and **R. H. Pollard.** 2000. Arctic fox den densities in the Prudhoe Bay oil field, Alaska. Canadian Field-Naturalist 114: 453–456.

Dietz, R., E. W. Born, C. T. Agger, and **C. O. Nielsen.** 1995. Zinc, cadmium, mercury, and selenium in polar bears (*Ursus maritimus*) from central east Greenland. Polar Biology 15: 175–185.

Helsel, R. R. 1990. Less than obvious. Statistical treatment of data below the detection limit. Environment Science Technology 24: 1766–1774.

Kolenosky, G. B. 1987. Polar bear. Pages 475-485 *in* Wild Furbearer management and conservation in North America. *Edited by* M. Novak, J. A. Baker, M. E. Obbard, and B. Mallock. Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Newman, M. C., K. D. Greene, and **P. M. Dixon.** 1995. Uncensor v 4.0. Savannah River Ecology Laboratory, Aiken, South Carolina. 91 pages.

Norstrom, R. J., R. E. Schweinsberg, and **B. T. Collins.** 1986. Heavy metals and essential elements in livers of polar bear (*Ursus maritimus*) in the Canadian arctic. Science Total Environment 48: 195–212.

Pollard, R. H., W. B. Ballard, L. E. Noel, and **M. A. Cronin.** 1996. Parasitic insect abundance and microclimate of gravel pads and tundra within the Prudhoe Bay oil field, Alaska, in relation to use by caribou. Canadian Field-Naturalist 110: 649–658.

Prestrud, P., G. Norheim, T. Silvertsen, and **H. L. Daae.** 1994. Levels of toxic and essential elements in arctic fox in Svalbard. Polar Biology 14: 155–159.

Smith, T. G., and **F. A. J. Armstrong.** 1975. Mercury in seals, terrestrial carnivores, and principal food items of the Inuit, from Holman, N.W.T. Journal of Fisheries Research Board of Canada 32: 795–801.

Snedecor, G. W., and **W. G. Cochran.** 1980. Statistical methods. Iowa State University Press. Ames, Iowa. 593 pages.

Stubblefield, W. A., A. S. Cohen, D. D. Gulley, J. Colonell, C. L. Fordham, K. E. Klima, P. Hampton, and **R. Jakubczak.** 1992. Potential bioaccumulation of reserve pit constituents in tundra biota on Alaska's North Slope. Presentation at North Slope Terrestrial Studies Workshop, 13-14 February 1992. Anchorage, Alaska.

Received 27 December 2000
Accepted 29 May 2003

Winter Occurrence of Harlan's, *Buteo jamaicensis harlani*, and Krider's, *B. j. borealis*, Hawks in Eastern Kansas

ROGER D. APPLEGATE[1] and DEBORAH R. APPLEGATE[2]

[1]Kansas Department of Wildlife and Parks, Research and Survey Office, P. O. Box 1525, Emporia, Kansas 66801-1525 USA
[2]627 Rural Street, Emporia, Kansas 66801 USA

Applegate, Roger D., and Deborah R. Applegate. 2003. Winter occurrence of Harlan's, *Buteo jamaicensis harlani*, and Krider's, *B. j. borealis*, hawks in eastern Kansas. Canadian Field-Naturalist 117(1): 122–123.

We counted Red-tailed Hawks (*Buteo jamaicensis*) on 27 roadside routes in eastern Kansas from September – March 1997-2003. Harlan's Hawks (*B. j. harlani*) comprised 1.1% and Krider's Hawks (*B. j. borealis*) were 0.3% of a total of 5 994 for all Red-tailed Hawks counted.

Key Words: Red-tailed Hawk, *Buteo jamaicensis,* Harlan's Hawk, *Buteo jamaicensis harlani,* Krider's Hawk, *Buteo jamaicensis borealis,* Kansas, winter.

The Red-tailed Hawk (*Buteo jamaicensis*) is the most abundant winter raptor in Kansas (Williams et al. 2000). Harlan's Hawk (*B. j. harlani*) is one of several subspecies of the Red-tailed Hawk that occurs in eastern Kansas. The subspecific status has been documented by Mindell (1983). Krider's Hawk is a color morph of the Eastern Red-tailed Hawk (*B. j. borealis*) (Wheeler and Clark 1995). Previously, the AOU (1957) and Godfrey (1986) accepted Krider's Hawk as a valid subspecies.

In a study in north-central Oklahoma (Lish and Burge 1995), Harlan's Hawks and Krider's Hawks represented 5.4% and 0.1%, respectively, of all Red-tailed Hawks counted on a 27.3 km roadside route. Red-tailed Hawks concentrate along roadsides because of available perch sites, habitat, and associated prey (Cox 1976; Finfrock 1976). We report the occurrence of Harlan's and Krider's hawks in eastern Kansas during winter.

Methods

We conducted road counts of raptors, September – March 1997-2001, on 27 routes that were 4.8 to 389.4 km in length. Routes were located within the Flint Hills and Osage Cuestas physiographic provinces (Wilson 1978). We drove the routes at existing maximum speed limits for the roads being traveled (97-112 kph) and as with Finfrock (1976) we did not make stops. All Red-tailed Hawks were identified by comparison with the illustrations in Clark and Wheeler (1987) and Wheeler and Clark (1995). We included only red-tails for which we were confident of identification. Unidentified raptors were counted as unknown.

Results and Discussion

During 240 counts we recorded 5 994 total Red-tailed Hawks. Harlan's Hawks (N = 63) were recorded during 49 counts (20.4%) and represented 1.1% of all red-tails counted. Krider's Hawks (N = 18) were recorded during 13 counts (5.4%) and represented 0.3% of all red-tails counted.

Based on this study, the incidence of Harlan's Hawks in Kansas is lower than reported for Oklahoma, and the incidence of Krider's is similar (Lish and Burge 1995). The Harlan's Hawk migrates from Alaska and northwestern Canada to winter in the southeastern portion of the Great Plains including Kansas (Wheeler and Clark 1995; Sibley 2000). The Eastern Red-tailed Hawk, which includes the Krider's morph, is resident from the central Great Plains south to the Gulf coast and from the eastern edge of the Rocky Mountains to the Atlantic seaboard, with birds nesting in southcentral Canada and the northern Great Plains migrating southward for the winter (Wheeler and Clark 1995; Sibley 2000). These data suggest that Harlan's Hawks winter in higher numbers in a gradient from Kansas south into Oklahoma. Krider's Hawks, on the other hand, winter across a wider front.

Acknowledgments

This project was supported by the Kansas Department of Wildlife and Parks and the authors. We thank B. E. Flock and K. R. Van Why for assistance with raptor counts. Suggestions provided by J. Lish are greatly appreciated.

Literature Cited

AOU. 1957. Checklist of North American birds. American Ornithologists Union, Washington, DC. 691 pages.

Clark, W. S., and **B. K. Wheeler.** 1987. A field guide to hawks: North America. Houghton Mifflin Company, Boston. 198 pages.

Finfrock, A. M. 1976. Winter hawk distribution: the effect of roadside management techniques. M. S. thesis, University of Kansas, Lawrence, Kansas. 88 pages.

Godfrey, W. E. 1986. The birds of Canada. Revised edition. National Museums of Canada, Ottawa, Ontario. 595 pages.

Lish, J. W., and **L. J. Burge.** 1995. Population characteristics of red-tailed Hawks wintering on tallgrass prairies in Oklahoma. Southwestern Naturalist 40: 174–179.

Mindell, D. P. 1983. Harlan's hawk, *Buteo jamaicensis harlani*, as valid subspecies. Auk 100: 161–167.

Sibley, D. A. 2000. The Sibley guide to birds. Alfred A. Knopf, New York. 544 pages.

Wheeler, B. K., and **W. S. Clark.** 1995. A photographic guide to North American raptors. Academic Press, San Diego. 198 pages.

Williams, C. K., **R. D. Applegate**, **R. S. Lutz**, and **D. H. Rusch**. 2000. A comparison of raptor densities and habitat use in Kansas cropland and rangeland ecosystems. Journal of Raptor Research 34: 203-209.

Wilson, F. W. 1978. Kansas landscapes: a geologic diary. Educational Series 5, Kansas Geological Survey, University of Kansas, Lawrence. 50 pages.

Received 15 February 2001
Accepted 7 July 2003

Feral Dogs, *Canis familiaris*, Kill Coyote, *Canis latrans*

JAN F. KAMLER[1], KURT KEELER[2], GALEN WIENS[2], CHAD RICHARDSON[3], AND PHILIP S. GIPSON[4]

[1]Polish Academy of Sciences, Mammal Research Institute, 17-230 Białwieża, Poland
[2]Smoky Hill Air National Guard Range, 8429 West Farrelly Road, Salina, Kansas 67401 USA
[3]U.S.D.A.-A.P.H.I.S. Wildlife Services, 232 Ackert Hall, Kansas State University, Manhattan, Kansas 66506 USA
[4]Kansas Cooperative Fish and Wildlife Research Unit, 205 Leasure Hall, Division of Biology, Kansas State University, Manhattan, Kansas 66506 USA

Kamler, Jan F., Kurt Keeler, Galen Wiens, Chad Richardson, and Philip S. Gipson. 2003. Feral dogs, *Canis familiaris*, kill Coyote, *Canis latrans*. Canadian Field-Naturalist 117(1):123–124.

We observed and photographed the attack and killing of a Coyote (*Canis latrans*) by a pack of three feral Dogs (*Canis familiaris*). Although interspecific predation is not uncommon among canid species, our observation represents the first published documentation of a Coyote mortality caused by feral Dogs.

Key Words: Coyote, *Canis latrans*, feral Dog, *Canis familiaris*, predation, Kansas.

Interspecific predation is common among canid species (Peterson 1995), however, there are no published records of predation on Coyotes (*Canis latrans*) by feral Dogs (*Canis familiaris*). During late morning in June 1992, one of us (KK) heard Dogs barking in the distance while working on Smoky Hill Air National Guard Range (Smoky Hill) in Saline County, Kansas (38°60′N, 97°85′W). Keeler walked a short distance to determine where the barking Dogs were located, and then observed and photographed the following. A pack of three feral Dogs had a Coyote cornered under a low hanging tree. All three Dogs were large (> 20 kg) and appeared to be mixed breeds; two were dark and appeared to be part Labrador Retriever, and the third was light-colored and appeared to be part Pyrenees. For several minutes the three feral Dogs repeatedly charged and attempted to bite the Coyote. After numerous attacks, the Coyote fled from the feral Dogs, however, the light-colored Dog pursued and caught the Coyote within 10 m. This Dog, the largest of the three, grabbed the Coyote along the spine near the hips and appeared to sever the spinal cord. The Coyote became limp and apparently was dead before the remaining two Dogs caught up to the first Dog. The three feral Dogs then sniffed the Coyote carcass for several seconds then slowly trotted away together. Photographs are stored at the Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University, Manhattan.

The vegetative community on Smoky Hill, 13 700 ha, is dominated by tall and mixed-grass prairies interspersed with wooded ravines and drainages. Feral Dogs are rarely observed on Smoky Hill. These three feral Dogs were not observed on Smoky Hill before this incident, however, we observed them several months later with three additional feral Dogs in their pack. We classified these Dogs as feral because they were not observed near human habitation, they were not wearing collars, and they avoided human contact (Scott and Causey 1973; Gipson 1983; Green and Gipson 1994).

Interspecific conflicts, including predation, are well documented among canid species. For example, Wolves are known to kill Coyotes (Carbyn 1982; Crabtree and Sheldon 1999), Red Foxes (*Vulpes vulpes*) (Peterson 1995), and tame domestic Dogs (Fritts and Paul 1989). Coyotes are known to kill Red Foxes (Sargeant and Allen 1989), Kit Foxes (*Vulpes macrotis*) (Ralls and White 1995), Swift Foxes (*Vulpes velox*) (Sovada et al. 1998), and tame domestic Dogs (Bider and Weil 1984). Prior to our observation, only Red Foxes were reportedly killed by feral Dogs (Pils and Martin 1974), although tame domestic Dogs can be trained to pursue and kill Coyotes for sport hunting (Andelt 1987).

Feral Dogs may not be as efficient predators as Wolves or Coyotes (Gipson and Sealander 1977), but they can occupy similar niches (Scott and Causey 1973) and may compete with native canids for resources. In Europe, feral Dogs compete with Wolves for limited food and space (Boitani 1983). In North America, feral Dogs were shown to have diets similar to Coyotes (Gipson and Sealander 1976), suggesting that these two species may compete for food resources. Our observation shows that feral Dogs can kill Coyotes, and suggests that feral Dogs may compete with Coyotes for space. This might especially be true when feral Dogs form packs and have large body sizes, which would give them an advantage over Coyotes in territorial disputes.

Literature Cited

Andelt, W. F. 1987. Coyote predation. Pages 128-140 *in* Wild Furbearer Management and Conservation in North America. *Edited by* M. J. Novak, J. A. Baker, M. E. Obbard, and B. Malloch. Ministry of Natural Resources, Ontario.

Bider, J. R., and **P. G. Weil.** 1984. Dog, *Canis familiaris,* killed by a Coyote, *Canis latrans*, on Montreal Island, Quebec. Canadian Field-Naturalist 98: 498–499.

Boitani, L. 1983. Wolf and dog competition in Italy. Acta Zoologica Fennica 174: 259–264.

Carbyn, L. N. 1982. Coyote population fluctuations and spatial distribution in relation to wolf territories in Riding Mountain National Park, Canada. Canadian Field-Naturalist 96: 176–183.

Crabtree, R. L., and **J. W. Sheldon.** 1999. Coyotes and canid coexistence in Yellowstone. Pages 127-163 *in* Carnivores in ecosystems: the Yellowstone experience. *Edited by* T. M. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva. Yale University Press, New Haven, Connecticut.

Fritts, S. H., and **W. J. Paul.** 1989. Interactions of wolves and dogs in Minnesota. Wildlife Society Bulletin 17: 121–123.

Gipson, P. S. 1983. Evaluation and control implications of behavior of feral dogs in interior Alaska. Vertebrate Pest Control and Management Materials 4: 285–294.

Gipson, P. S., and **J. A. Sealander.** 1976. Changing food habits of wild *Canis* in Arkansas with emphasis on coyote hybrids and feral dogs. American Midland Naturalist 95: 249–253.

Gipson, P. S., and **J. A. Sealander.** 1977. Ecological relationships of white-tailed deer and dogs in Arkansas. Pages 3-16 *in* Proceedings of the Predator Symposium. *Edited by* R. L. Phillips and C. Jonkel. University of Montana, Missoula.

Green, J. H., and **P. S. Gipson.** 1994. Feral dogs. Pages C77-81 *in* Prevention and control of wildlife damage. *Edited by* S. E. Hygnstrom, R. M. Timm, and G. E. Larson. Cooperative Extension Division, University of Nebraska, Lincoln; U.S.D.A.-A.P.H.I.S. Wildlife Services; and Great Plains Agricultural Council, Wildlife Committee.

Peterson, R. O. 1995. Wolves as interspecific competitors in canid ecology. Pages 315-323 *in* Ecology and conservation of wolves in a changing world. *Edited by* L. N. Carbyn, S. H. Fritts, and D. R. Seip. Canadian Circumpolar Institute, Edmonton, Alberta.

Pils, C. M., and **M. A. Martin.** 1974. Dog attack on a communal fox den in Wisconsin. Journal of Wildlife Management 38: 359–360.

Ralls, K., and **P. J. White.** 1995. Predation on endangered San Joaquin kit foxes by larger canids. Journal of Mammalogy 76: 723–729.

Sargeant, A. B., and **S. H. Allen.** 1989. Observed interactions between coyotes and red foxes. Journal of Mammalogy 70: 631–633.

Scott, M. D., and **K. Causey.** 1973. Ecology of feral dogs in Alabama. Journal of Wildlife Management 37: 253–265.

Sovada, M. A., C. C. Roy, J. B. Bright, and **J. R. Gillis.** 1998. Causes and rates of mortality of Swift Foxes in western Kansas. Journal of Wildlife Management 62: 1300–1306.

Received 5 February 2001
Accepted 23 June 2003

Vegetation Classification Standard for Canada Workshop: 31 May–2 June 2000

Rob Alvo[1] and Serguei Ponomarenko[2]

[1]58, GAVIA Biological Services, rue des Parulines, Gatineau, Québec J9A 1Z2 Canada
[2]NatureServe Canada, c/o Ecological Integrity Branch, Parks Canada, 25 Eddy St., Gatineau, Quebec K1A 0M5 Canada

Alvo, Rob, and Serguei Ponomarenko. 2003. Vegetation Classification Standard for Canada Workshop: 31 May–2 June 2000. Canadian Field-Naturalist 117(1): 125–139.

The workshop, "Vegetation Classification Standard for Canada" was held in Hull (now Gatineau), Quebec, 31 May–2 June 2000. Representatives from a wide spectrum of Canadian federal agencies, territorial and provincial agencies, and conservation organizations throughout Canada, as well as representatives from the U.S. and Mexico, participated. The 20 presentations covered: the importance of a national vegetation classification; the International Classification of Ecological Communities (ICEC); history of the Canadian project; review of classification work in Canada; the status of vegetation classifications in the Canadian territories and provinces, along with some case studies; the development of a Canadian Forest Ecosystem Classification (FEC); and, a proposal for a Canadian National Vegetation Classification (CNVC). Two key decisions made at the workshop were that (1) the ICEC should be the basis from which to develop a CNVC as a standard, and (2) a CNVC Working Group should be established and consist of two sub-groups: a Steering Committee and a Technical Committee. We anticipate that decisions made at and after this workshop will have a substantial impact on how ecological communities are classified and used for conservation throughout Canada and beyond.

Key Words: classification, vegetation, natural community, standard, workshop, International Classification of Ecological Communities.

Efforts to protect and manage biodiversity and natural resources often focus on the ecosystem level because this level can encompass genes, species, and species assemblages, as well as the ecosystem resources, processes, and interactions that they depend on. These efforts would benefit from a standard system for classifying and naming ecosystems or ecological communities. A set of standards would aid resource inventory, planning, conservation, monitoring, restoration, and other activities by allowing them to take place and be understood across, rather than only within, political or administrative boundaries.

There exist a large number of local, national and international ecosystem classifications using a variety of concepts to develop standards for classification. Where the focus of classification is on the protection of biological diversity, classifications that focus on the biotic components of ecosystems (biocoenoses or biological communities) have great merit in that they are inherently directly relevant to biodiversity. Vegetation is typically the most readily classifiable component of terrestrial ecological communities, and vegetation classifications have been widely used in a number of systems throughout the world.

Currently there are two centres of fast expanding international vegetation community classifications. The first, often called the Braun-Blanquet system (Braun-Blanquet 1928; Westhoff and van der Maarel 1980), now embraces twenty-five European and Asian countries, and is a strongly floristically-based system. The second is in North America, where NatureServe and The Nature Conservancy (TNC), both international non-governmental organizations, have developed the International Classification of Ecological Communities (ICEC) (Grossman et al. 1998). This is a joint physiognomic-floristic classification system with a strong emphasis on conservation applications. Only the U.S. terrestrial portion of this classification is currently well-developed. The Braun-Blanquet and the ICEC systems use similar floristic concepts, the *association* and the *alliance*, to define the vegetation units.

Canada also needs a standard national ecological community classification because the country must address biodiversity and natural resource conservation requirements that are increasingly being enshrined in international and domestic legislation and that are largely the responsibility of different levels of government (local, provincial/territorial, and federal). Use of the classification would allow the efforts of different jurisdictions to be prioritized and compared. Because the requirements apply to the entire global ecosystem, the classification ultimately must include all types of natural communities (marine, freshwater, terrestrial, subterranean, and possibly aerial).

On 31 May–2 June 2000, Parks Canada, the Canadian Forest Service (CFS), NatureServe, TNC, and World Wildlife Fund (Canada) (WWF) held a workshop in Hull (now Gatineau), Quebec to initiate a major new effort to establish a national ecological community classification for Canada. Participants from a wide spectrum of Canadian federal agencies, provincial agencies, and conservation organizations

throughout Canada, as well as representatives from the U.S., participated in the workshop called, "Vegetation Classification Standard for Canada".

Present at the Workshop

Peter Achuff (Parks Canada, Jasper National Park), **Hussein Alidina** (WWF Canada), **Lorna Allen** (Alberta Natural Heritage Information Centre), **Rob Alvo (RA)** (Parks Canada), **Marilyn Anions** (Canadian Wildlife Service), **Harry Archibald** (Alberta Environment), **Wasyl Bakowsky** (Ontario Natural Heritage Information Centre), **Ken Baldwin** (CFS), **Sean Blaney** (Atlantic Canada Conservation Data Centre (AC CDC)), **Don Faber-Langendoen** (NatureServe), **Vincent Gérardin** (Ministère de l'Environnement du Québec), **Ann Gerry** (Saskatchewan CDC), **Jason Greenall** (Manitoba CDC), **Dennis Grossman** (NatureServe), **Ole Hendrickson** (Biodiversity Convention Office), **Jürgen Hoth** (Commission on Environmental Cooperation), **Catherine Kennedy** (Yukon Department of Renewable Resources), **Paula Kigjugalik Hughson** (Parks Canada), **Gildo Lavoie** (Centre de données sur le patrimoine naturel du Québec), **Nik Lopoukhine** (Parks Canada), **Bill Meades** (CFS), **Del Meidinger** (British Columbia Ministry of Forests), **Bas Oosenbrug** (Northwest Territories Department of Resources, Wildlife and Economic Development), **Serguei Ponomarenko (SP)** (Parks Canada), **John Riley** (Nature Conservancy of Canada), **Jean-Pierre Saucier** (Forêt-Québec), **Peter Uhlig** (Ontario Ministry of Natural Resources), and **Alan Weakley** (NatureServe).

Workshop Presentations

Values of a Standardized International Classification of Ecological Communities (Alan Weakley — NatureServe)

In general, standardized taxonomies are widely used in human enterprises because they allow effective communication about the units in question. Communities, ecosystems, and landscapes are increasingly recognized as important, even critical, units for conservation analysis, planning, and management (Grossman et al. 1998; Anderson et al. 1999; Maybury 1999; Stein et al. 2000).

In North America, many different approaches to community classification have been taken, and individual provinces, states, and countries have developed independent and incompatible systems, which is hampering collaboration and communication across geopolitical borders. For the last 15 years, TNC and collaborators (now including NatureServe) have been developing a consistent, standardized, hierarchical community classification for the U.S. and other parts of the Americas, based on the UNESCO physiognomic classification at upper hierarchical levels and floristically based lower hierarchical levels: the ICEC (Grossman et al. 1998). This is facilitating: flexibility of application at different scales and for different purposes; comparison across boundaries and agencies; development of methods and databases; efficient development and application utilizing available information and classifications; and, use of remote-sensing data. The ICEC is a standard in the U.S., and is in active use by TNC, the network of Natural Heritage Programs (NHPs) and Conservation Data Centres (CDCs), and most land-managing agencies in the U.S. As its use increases and expands, and as additional data are developed for all the classification units (e.g., rarity, threats, associated rare species, management needs), its benefits should expand.

Importance of a Canadian National Vegetation Classification (CNVC) in Canada (Nik Lopoukhine — Parks Canada)

Biodiversity classification at the ecosystem level for all lands and waters under Canada's jurisdiction was made a high priority by the Canadian Biodiversity Strategy (Biodiversity Convention Office 1995) when it discussed the need for: "determining the status of ecosystems, species, and genetic resources." It also recognized that protection of biological diversity would require a new approach to managing ecosystems.

Numerous detailed ecosystem classifications exist on local or provincial levels. Classifications in Canada use different hierarchical structures, categories, and terminology. Some were developed for very specific purposes and are focused on a few properties of natural communities, so they cannot easily be used for biodiversity conservation. Others deal only with forests or wetlands.

The Canadian Biodiversity Science Board recently stated that the development of a Canadian Ecosystem Community Classification is a high priority. The National Forest Strategy also identifies "ecosystem classification" as one of four top priorities, and the CFS has initiated a national forest classification for Canada. There is as yet no comparable effort for other major ecosystems (e.g., grasslands, tundra) at the national level, although numerous provincial or territorial classification projects exist. In order to satisfy the requirement of the Convention to "identify components of biological diversity" on an ecosystem level, what is needed is a comprehensive classification of all terrestrial ecosystems throughout Canada that is applicable to all the major types of ecosystems, including forests, grasslands, wetlands, and tundra.

Having a standard ecosystem classification would allow Canada to:

- Undertake inventories of terrestrial ecosystems at selected levels of precision and to compare the results of these inventories with those of other countries and with future Canadian inventories. Thus, endangered, declining, and

common ecosystems could be consistently identified at local, provincial, national, and international levels, and adequate measures to preserve biodiversity at the ecosystem level could be planned, evaluated, compared, and undertaken at all these levels.
- Report on and analyze the status of Canadian ecosystems, including at the international level.
- Develop a representative system of protected areas.
- Evaluate the cost effectiveness of ecosystem conservation measures.

and allow Parks Canada to:

- Develop a single system of vegetation inventory, mapping, monitoring and analysis in a national park system.
- Identify how well represented different ecosystem types are in national parks, and identify gaps to help in planning of new national parks.
- Develop a vegetation community database within the national park system.

History of the International Classification of Ecological Communities (Dennis Grossman — NatureServe)

The International Classification of Ecological Communities (ICEC) grew out of a longstanding recognition on the part of The Nature Conservancy (TNC) and the Natural Heritage Program (NHP)/ Conservation Data Centre (CDC) network that ecological communities were important elements of conservation. These organizations employ what is often referred to as a "coarse filter/fine filter" approach to preserving biological diversity (Jenkins 1976; Hunter 1991). This involves the identification and protection of the best examples of all ecological communities (coarse filter) as well as rare species (fine filter). Identifying and protecting representative examples of ecological communities assures the conservation and maintenance of biotic interactions and ecological processes, in addition to conservation of most species. Certain species, however, usually the rarest ones, may fall through the community filter. Very rare species often have specialized life histories, or are simply so rare and restricted that their conservation requires explicit planning based on species-specific information. Identification and protection of viable occurrences of rare species serves as the fine filter for preserving biological diversity. Using both filters for identifying conservation targets ensures that the most complete spectrum of biological diversity is protected.

In the U.S., state community classifications were developed for many states by the NHP ecologists, with each state using its own classification scheme. This approach worked effectively at a state level to assure protection of ecological communities. However, a major obstacle to using communities as conservation units at the regional, national, and global levels was the lack of a consistent classification system developed through analysis of data from a range-wide perspective. To overcome this problem, TNC and the NHP/CDC network began working to develop a standardized, hierarchical system to classify vegetated terrestrial communities across the U.S.

The first steps taken by TNC regional ecologists were to begin compiling an enormous amount of fine-scale state and local information on vegetation patterns into four regional classifications spanning the U.S. and to decide upon a single, standardized framework for the classifications they were developing. The U.S. regional classifications were; of necessity, developed somewhat independently. In the western U.S., for example, most of the existing state classifications were based on vegetation and were strongly influenced by the habitat type approach, which allowed a relatively straightforward compilation into a regional classification for the west. In the Midwest, East, and Southeast, however, there was less of a tradition of floristically-based classifications, and, as a result, there was more emphasis on a synthesis of descriptive information on vegetation, often done with close consultation and review by Heritage program ecologists, along with other partners in state and federal agencies, and university scientists.

Synthesis of the four regional classifications into a U.S. National Vegetation Classification was completed and the first iteration of that classification was published (Anderson et al. 1998). While classification development has so far focused on the U.S. (and is continuing there), classification of Canadian vegetation using the ICEC is proceeding quickly, as is classification of the vegetation of portions of northern Mexico. Caribbean vegetation has also been an area of recent classification development, and some classification at finer levels has also been done for southeastern Alaska.

The following basic tenets underlie the terrestrial portion of the ICEC:
- It is based primarily on vegetation, rather than on soils, landforms or other non-biologic features.
- It applies to all terrestrial vegetation. In addition to upland vegetation, "terrestrial vegetation" is defined to include all wetland vegetation with rooted vascular plants, and communities with sparse to nearly absent vegetation cover.
- It focuses on existing vegetation rather than on potential natural or climax vegetation.
- While it can be used to classify all vegetation, emphasis has been given to vegetation types that are natural or near-natural.

The top division of the classification hierarchy separates vegetated communities (Terrestrial System) from those of unvegetated deepwater habitats (Aquatic System) and unvegetated subterranean habitats (Subterranean System). The Terrestrial System is broadly defined to include areas with rooted submerged vegetation of lakes, ponds, rivers, and marine shorelines, as well as the vegetation of uplands.

The hierarchy for the Terrestrial System has seven levels: the five highest (coarsest) levels are physiognomic and the two lowest (finest) levels are floristic. The physiognomic portion of the ICEC hierarchy is a modification of the UNESCO (1973) world physiognomic classification of vegetation, and it incorporates some of the revisions that have been made during the past thirty years.

Partners in Developing the International Classification of Ecological Communities (ICEC) — a Case Study with Emphasis on the Southeastern United States (Alan Weakley — NatureServe)

In the southeastern U.S., a partnership between NatureServe/TNC, the NHP/CDC network, academics, and land-managing agencies, is developing and applying the ICEC. This has been mutually beneficial: resources are pooled and greater progress can be made than if each political unit and organization were developing its own classification. The U.S. Departments of Agriculture (Forest Service)(USFS), Defense, and Energy, the U.S. Fish and Wildlife Service, the Tennessee Valley Authority and other agencies have also participated in the development and application of the ICEC.

To date, the USFS has supported: Southeast Region classification and community descriptions; characterization of vegetation for the Ecological Classification System at province, section, and subsection levels; ranking of conservation status of associations; characterization and definition of old growth forests; priority-setting for Research Natural Area and Special Interest Area designations, based on the classification; ecosystem management in the Columbia River Basin; and, development of databases and analysis systems to support the development and use of the ICEC. The largest land-managing agency in the U.S., the USFS sees the classification as providing a basis for: ecosystem management; adaptive management; sustainability; forest planning; land management and stewardship (fire, thinning, restoration, etc.); characterization of wildlife habitats (e.g., big game); characterization of habitats for federally listed Threatened, Endangered, and Sensitive species; characterization of stand types or dominant cover for forest inventories; assessment of conservation needs for both rare and representative community types; and, efficient and standardized development of USFS Ecological Classification for National Forest lands.

The Gap Analysis Program (GAP) is mapping the vegetation of the U.S., state by state, primarily at the alliance level. This provides a basis for habitat modeling for vertebrate and other selected species. The National Park Service is mapping existing vegetation types on all its lands using aerial photography and the ICEC, primarily at the association level. Both initiatives are occurring nation-wide.

History of the Canadian Project (Rob Alvo — Parks Canada)

In the 1990s, SP and RA were aware that there was a need for a national vegetation classification in Canada. They met in 1998 when both were volunteering for Parks Canada. SP had visited The Nature Conservancy (TNC) in 1994 while on an internship from Russia, where he had been working for World Wildlife Fund (WWF) as Forest Officer. RA had helped establish the first Canadian Conservation Data Centre (CDC), in Quebec, from 1988 to 1991. Thus, both were familiar with the work of the TNC "Heritage" network and the fact that the network used vegetation classifications to help them decide which natural areas to recommend for protection. Both were also aware that the network, which eventually became NatureServe, had developed a terrestrial vegetation classification for the U.S. and knew that there was no similar initiative in Canada. They also agreed that such an initiative could be very useful for the conservation of biodiversity in Canada.

They spoke with several people to see whether interest in developing a classification for Canada could be generated. Nik Lopoukhine, a vegetation ecologist himself and then Director of the Ecosystems Branch at Parks Canada (now the Ecological Integrity Branch), supported the idea and provided SP office space so that he and RA could prepare a proposal. Claude Mondor, Chief of Area Identification at Parks Canada, Ole Hendrickson, then the Senior Science Advisor at the Canadian Forest Service (CFS), and Dennis Grossman, then Chief Ecologist at NatureServe, all reacted positively. The CFS had been attempting to develop a Canadian Forest Ecosystem Classification, and saw this project as providing a framework for it.

Nik contracted SP and RA to complete the proposal, called "Proposal to Develop a Framework for a Canadian Ecosystem Classification for Biodiversity Conservation". This was completed on 24 November 1998.

A background paper was required to present the position that a vegetation classification was needed in Canada. In early 1999, Nik identified funds to pay SP to write it. Bill Meades, Director of Forest Ecology for the CFS, matched Parks Canada's contribution. WWF (Canada) also made a contribution.

In 1999, SP and RA prepared a report called, "Perspectives on Developing a Canadian Classification of Ecological Communities" (Ponomarenko and Alvo 2000), published by the CFS. An abridged version with additions, called, "Developing a Canadian National Vegetation Classification" (Ponomarenko et al. 2000*), was prepared for the workshop.

Dennis Grossman suggested that a workshop be organized to bring important players together from throughout Canada, as well as key people from

NatureServe, to explore the idea of developing a Canadian National Vegetation Classification (CNVC). Parks Canada and the CFS met in December 1999 and decided to set up a steering committee to organize the workshop. They contracted SP to organize the workshop with RA, who had become a Parks Canada employee.

In the early stages of the project, the late Don McAllister (Canadian expert on fishes and later avid conservationist) was contacted regarding the question of a marine classification. He had been working on a marine classification for the Pacific coast of Canada (McAllister 2000) and was very interested in seeing a complete ecological classification for Canada that would include not only the terrestrial system, but also the marine, freshwater and subterranean systems. It was agreed that the project should first concentrate on the terrestrial system, but that a major long-term goal should be the development of classifications for the other systems.

Review of Existing Classification Efforts in Canada (Serguei Ponomarenko — Canadian Vegetation Classification Project)

The early works of Halliday (1937) and Rowe (1959) outlined very broad forest regions and districts in Canada. More detailed classifications at the natural community level for local areas were later developed in the west by Krajina (1959, 1960, 1965, 1969), who combined Russian and European traditions, and in the east by Dansereau (1959), Grandtner and Vaucamps (1982) and others, who followed the Braun-Blanquet approach.

In the 1960s to the 1980s, many efforts were made to develop an Ecological Land Classification (ELC) (Ecological Stratification Working Group 1993, 1995*) that would be a landscape regionalization system. At the same time, some provinces developed their own landscape regionalization systems that were not always compatible, neither among themselves nor with the Canadian ELC.

In the late 1980s and the 1990s, most Canadian provinces and territories, with the CFS, developed FECs. Now there are more than 50 FECs in the country. These systems, which work well at the local level, are not compatible with each other and cannot be easily merged. Nevertheless, it was by using these classifications that considerable information useful in developing a national standard classification was amassed. A set of "dictionaries" was required to "cross-walk" (i.e., translate) local FECs into a national standard at the lowest level of the hierarchy (*association*) or at the second level (*alliance*). Recently, the CFS started developing a Canadian FEC (see below).

In 1990, The National Vegetation Working Group of Canada Committee on ELC proposed an outline of a Canadian vegetation community classification (National Vegetation Working Group 1990*). Unfortunately, this eminent event was never followed up at the national level. The proposed floristic levels of this system were never developed.

Another classification developed at the national level is a Canadian Wetland Classification by the National Wetlands Working Group (1987). The lowest level of this system is wetland type based on vegetation physiognomy, which can be cross-walked with the ICEC.

Several Canadian Conservation Data Centre classifications use the ICEC or are completely compatible with it at the lowest (*association*) level (Belcher 1994*; Bakowsky 1996*; British Columbia Conservation Data Centre 1996*; Greenall 1996*; Comer et al. 1999*). This classification approach is proposed (see below) as a basis for developing a Canadian National Vegetation Classification (CNVC). These and other Canadian classifications are reviewed by Ponomarenko and Alvo (2000) in more detail.

Status of Vegetation Classification in the Yukon (Catherine Kennedy, Yukon Department of Renewable Resources)

The Yukon is a vast, sparsely populated wilderness, extending from the boreal forest to the Arctic Ocean. Although species diversity is lower than in warmer regions of Canada, there is a notable diversity of landscapes and biomes. Most vegetation types remain in a natural state, unaltered by human activities, and the flora includes many successional phases due to frequent wildfires (Viereck and Schandelmeier 1980*) and limited fire suppression.

Vegetation classification in the Yukon has a relatively recent history, spanning only the past 25 years. This work began with the ELC programs of the 1970s (Wiken et al. 1981) and continued with the development of *Ecoregions of the Yukon* (Oswald and Senyk 1977*), which was revised in 1995 (Ecological Stratification Working Group 1995*). Detailed vegetation surveying has continued at various locations throughout the territory on a project-specific basis, rather than on a systematic inventory basis.

Although vegetation surveying has been relatively limited due to the resources required in very rugged and remote terrain, there is good geographical and ecological representation of the Yukon's characteristic terrestrial vegetation communities, both forested and non-forested. Most vegetation data are accompanied by data on soil and site characteristics. To date, one field guide to ecosystem classification has been completed, for the southeast Yukon — it describes soil, vegetation and management units (Zoladeski et al. 1996).

A standardized national vegetation classification would greatly assist in the monitoring of vegetation between jurisdictions in northern latitudes, a region which is particularly susceptible to the effects of

climate change. There are indications that vegetation is undergoing rapid and significant change near the Yukon's Arctic coast (Kennedy et al. 2000*).

Vegetation Classification in the Northwest Territories (Bas Oosenbrug— NWT Department of Resources, Wildlife and Economic Development)

The Department of Resources, Wildlife and Economic Development (RWED), Government of the Northwest Territories (NWT) is using 1:1 million scale mapping for soil type (parent material and development), texture, and topography (Agriculture and Agri-Foods Canada 1998*), in conjunction with vegetation mapping from satellite imagery (Thiesenhausen and Veitch 1998*; Epp and Matthews 1998*; Zimmer et al. 1999*), to determine biophysical land units in NWT. Soil-based "landscape units" are used as a first approximation to describe the biological diversity of each of NWT's terrestrial ecoregions (Oosenbrug and Gah 1998*).

A workshop in Hay River, N.W.T., in 1995 brought forest ecology experts from British Columbia and Alberta together with RWED staff to construct an initial forest vegetation classification for NWT. Subsequently, in 1997, RWED adopted a classification scheme for both the forested and tundra regions of NWT, using Landsat™ satellite imagery and ground-truth site analysis. This system divides the land base into vegetated and non-vegetated terrain. Vegetated cover is divided into forest and non-forest vegetation. Non-forest vegetation is described as shrub (tall/low, open/closed), herbaceous (herbs, lichens, sphagnum bog, grasses/sedges), or wetland (floating/emergent vegetation, fens). Forest vegetation is considered either open or closed (40% closure) coniferous, deciduous or mixed forest. Open coniferous forest is further characterized by dominant species — Jack Pine (*Pinus banksiana*), Black Spruce (*Picea mariana*), White Spruce (*Picea glauca*), or undifferentiated conifers. Likewise, closed coniferous forest is dominated by Jack Pine (mature or young), Black Spruce, White Spruce, or undifferentiated conifers. Ground-truth sites often contain additional information on topography, slope, aspect and understorey ground cover.

Preliminary classification for most of NWT has been completed. The approach used by RWED is intended to conform to a national forest inventory design (Canadian Forest Service 2000*) and has been adapted for use in Wood Buffalo and Nahanni National Parks, as well as for vegetation studies conducted through the West Kitikmeot/Slave Society in the tundra region of the NWT.

Vegetation Classification in British Columbia (Del Meidinger — British Columbia Ministry of Forests, and Adolf Ceska — British Columbia Conservation Data Centre)

Understanding and classifying the vegetation diversity of British Columbia has an historical relationship with forest type classification; the latter dates back to the early 1900s (Whitford and Craig 1918) and was the main focus of vegetation classification work until the 1950s. After that, Krajina (1965, 1969) at the University of British Columbia and several researchers within the British Columbia Forest Service began working on more detailed site and ecosystem classifications of the vegetation of several regions. Subsequently, Krajina had many graduate students study the vegetation of certain areas (e.g., Coastal Western Hemlock (Orloci 1961); Interior Western Hemlock (Bell 1964); Mountain Hemlock (Brooke 1966, Peterson 1964); Sub-Boreal Spruce (Revel 1972). From this early work, the Biogeoclimatic Ecosystem Classification (BEC) was developed and adopted by the British Columbia Forest Service in the mid-1970s (MacKinnon et al. 1992). It is a system of ecological classification that integrates vegetation, climate, and site classifications (see the following workshop presentation).

Several of Krajina's students went on to universities or research organizations and continued to classify vegetation. K. Klinka and colleagues (British Columbia Forest Service and University of British Columbia) have continually produced classification reports for coastal areas (Klinka et al. 1996; Green and Klinka 1994) and, more recently, some northern hardwood (Krestov et al. 2000a) and Black Spruce (Krestov et al. 2000b) forests. M. Bell at the University of Victoria had many graduate students classify vegetation, e.g., Ceska (1979) (south coast wetlands) and Roemer (1972) (southeastern Vancouver Island).

Several other organizations also classified vegetation in various regions of the province: the southern grasslands were classified by Tisdale (1947), McLean and others of Agriculture Canada (McLean 1970; van Ryswyk et al. 1966); the British Columbia Ministry of Environment classified vegetation in several regions (e.g., Lea 1984; Clement 1981); E. Packee of the forest company MacMillan-Bloedel classified coastal forests into habitat types; and G. Bradfield at the University of British Columbia and his graduate students classified estuaries and other vegetation types.

The Research Branch, British Columbia Ministry of Forests, has captured all this vegetation classification information and much of the data for the development of the vegetation classification component of the BEC (Pojar et al. 1987; Meidinger and Pojar 1991). The BEC vegetation classification is the most comprehensive vegetation classification in the province, but it is not complete. The wetland classification is nearing completion (www.for.gov.bc.ca/research/becweb/subsite-wrec/index.htm). Further vegetation classification is required for early- to mid-successional forests and high subalpine and alpine vegetation. The provincial Ministry of Forests maintains a vegetation database of data and

classification units and is working with the CDC to provide a complete vegetation classification. At present, over 20 000 plots of full vegetation data have been entered into the database following a standard data collection protocol.

Classifying Vegetation within British Columbia's Biogeoclimatic Ecosystem Classification System (Del Meidinger — British Columbia Ministry of Forests)

Biogeoclimatic Ecosystem Classification (BEC) is a system of ecological classification that integrates three classifications: vegetation, climate, and site (Pojar et al. 1987; Meidinger and Pojar 1991). Vegetation classification provides the foundation for BEC and is therefore the most important step in ecosystem classification.

Vegetation classification follows the principles of the Braun-Blanquet classification system, with some modifications. What results is a hierarchical classification of vegetation units, with the plant association as the basic unit. Alliances, Orders and Classes are groups of *associations; sub-associations* are divisions. Units are differentiated by a "diagnostic combination of species", which is assessed by hierarchical testing of proposed units. The resultant classes have floristic and physiognomic affinities. *Associations* are named by two or three scientific names without the "suffixes" that are used in other applications of Braun-Blanquet classification.

Classification development in British Columbia has focused on mature to climax coniferous forests and wetlands of the interior. Initial classifications of other non-forested and hardwood forest *associations* have also been completed.

Vegetation classification has been conducted over the past 20 years (MacKinnon et al. 1992) and is continuing, as new data are collected or compiled from other sources. Over this time, what have we learned about vegetation classification? That data are important — otherwise the units are based on opinion and different ecological views; that peer review of vegetation tables results in a more accepted and ecologically sound classification than individual efforts; and, that an efficient data compilation and analysis system is important (http://www.for.gov.bc.ca/prupert/vpro97/).

Vegetation Classification in Alberta (Lorna Allen — Alberta Natural Heritage Information Centre)

Beginning with the pioneering studies of Raup (1928, 1935) and Moss (1932, 1944, 1952, 1953, 1955; Moss and Campbell 1947), Alberta has a rich history of vegetation studies. At present, Alberta Environment houses a database with over 17 000 vegetation plots, many with associated soils data. These data have been collected primarily in the forested areas of the province, and have been principally used in management-oriented site classification projects (e.g., Beckingham and Archibald 1996; Beckingham et al. 1996a). There is also a large body of inventory information on grassland areas, collected primarily for range management purposes, that is currently being input into a database for numerical classification later this year. Some studies, such as a series on the Rocky Mountain National Parks (e.g., Holland and Coen 1982; Achuff et al. 1997a*), have begun a systematic vegetation classification.

Vegetation Mapping of the Waterton-Glacier International Peace Park (Peter Achuff — Conservation Biologist, Jasper National Park)

Waterton Lakes National Park, Alberta and Glacier National Park, Montana are developing a common vegetation map for both parks using the ICEC. The basic classification unit is the vegetation association. The map will be at a scale of 1:12 000, with a minimum polygon size of about 0.5 ha, and a classification accuracy standard of 80% for each map unit, based on an independent field assessment of the mapping. Map units generally will be vegetation *alliances* rather than associations. Field sampling is designed using a gradsect (gradient transect) approach that stratifies the landscape based on geology, soils, elevation, slope aspect, and stand age. A minimum of 3–5 field plots will be sampled for each vegetation *association*, with more common associations likely having 30 or more plots. About 500 plots will be recorded in Glacier National Park.

Vegetation plot data for Waterton Lakes National Park will be based primarily on about 300 field plots from a recently completed ELC (Achuff et al. 1997a*) that mapped integrated units defined by characteristic combinations of geology/landform, soils, and vegetation. The Waterton Lakes National Park ELC was mapped at 1:20 000 with the map units being Ecosites in the Canadian ELC hierarchy. The Ecosites contain more than one vegetation association. The associations (vegetation types) are based on current vegetation and include both mature and seral communities. The Waterton Lakes National Park vegetation classification is part of a system common to Banff, Jasper, Kootenay, Mt. Revelstoke, Glacier, and Yoho national parks (Achuff et al. 1984a*, 1984b*, 1997a*, 1997b*; Holland and Coen 1982). The system is hierarchical with five structural classes (closed forest, open forest, shrub, low shrub, herb-dwarf shrub) and about 170 associations, and is conceptually compatible with the ICEC. Waterton Lakes National Park contains about 50 associations.

A multi-agency working group from the U.S. National Parks Service, the U.S. Geological Survey, TNC, the Montana NHP, and Parks Canada is merging the Waterton Lakes National Park vegetation classification with that of Glacier National Park using the ICEC and developing common mapping units. Photo-interpretation mapping will be done

separately by U.S. and Canadian teams and will be merged into a common Geographic Information System (GIS) coverage.

Status of Vegetation Classification in Saskatchewan (Ann Gerry — Saskatchewan Conservation Data Centre)

A number of projects are underway in Saskatchewan to develop classification systems for terrestrial vegetation. The Saskatchewan Conservation Data Centre (CDC) and the Forest Ecosystems Branch of Saskatchewan Environment and Resource Management (SERM) are working on the expansion and integration of non-forested and forested vegetation community classifications. The Saskatchewan Wetland Conservation Corporation has recently completed a project with the University of Montana to develop a riparian classification for Saskatchewan. The intent is to develop links between these systems to ensure the consistent and thorough documentation of the province's terrestrial vegetation types.

For the past several years the CDC has been working with partner CDCs throughout Canada and the U.S. and with NatureServe to develop the ICEC. The primary focus of the CDC has been to document the existence of non-forested vegetation types that occur in the ICEC and to add new types found in Saskatchewan.

The first approximation of forest ecosites developed for the province (Beckingham et al. 1996b) was based solely on data from the Mid Boreal Upland and Lowland ecoregions. SERM's Forest Ecosystems Branch is now modifying and expanding its Forest Ecosystem Classification (FEC) for Saskatchewan's Provincial Forests through the collection of new data from 2000 new plots spanning the province's forests.

The CDC is currently working on a project that will encourage the integration of the FEC with the classification of non-forested vegetation throughout the province. This involves the characterization of a broad range of vegetation types in a major protected area: Cypress Hills Inter-provincial Park. This pilot project has three major goals: the development of a general methodology for predictive vegetation mapping and species habitat modeling; the integration of a resource inventory and information management system for the park; and, the expansion and integration of a vegetation classification for Saskatchewan using a standard methodology and terminology.

History, Status and Applications of the ICEC in Manitoba (Jason Greenall — Manitoba Conservation Data Centre)

The Manitoba CDC has been developing a provincial vegetation classification since 1994, following the standards of the ICEC. In 1996, the CDC produced a provincial classification, Manitoba's Terrestrial Plant Communities (Greenall 1996*).

The Manitoba classification currently lists 174 ecological community types for the province, including both vegetated and sparsely vegetated types such as cliffs, beaches and mudflats. Summary descriptions and status ranks have been created for all community types using available information.

Peer-review workshops have been held to review and revise conservation status ranks for all prairie and parkland communities, and for boreal forest communities. Additional workshops will be held to complete the review process. There are currently 45 community types (26%) considered provincially rare to uncommon. Information gaps exist for many poorly documented community types believed to occur in Manitoba.

Ecological community occurrence information has been compiled largely on an opportunistic basis, but has been valuable for ecoregional planning efforts in the Northern Tallgrass Prairie ecoregion. This has allowed a number of important sites to be incorporated into the ecoregional plan using communities as a "coarse filter" to account for the biodiversity of the area as a whole.

Case Study — Incorporating the Manitoba Forest Ecosystem Classification into the Manitoba Conservation Data Centre Vegetation Classification (Jason Greenall — Manitoba Conservation Data Centre)

During the development of its vegetation classification, the Manitoba CDC relied on the Manitoba FEC (Zoladeski et al. 1995) to describe many of the province's boreal forest communities. The Manitoba FEC was modeled after the FEC for Northwestern Ontario (Sims et al. 1989*), and combines previously collected forest plot data from several sources, along with some data collected for this project. It classified Manitoba's boreal forest communities into 33 vegetation types occurring on 22 soil types.

The CDC classification follows the standards of the ICEC. Many sources were consulted to create a list of all community types thought to occur in Manitoba. CDC community types were cross-walked to FEC vegetation types where there seemed to be a match, and vegetation type descriptions were then used to compose element summaries.

A workshop of Manitoba ecologists recommended a number of revisions to the CDC classification based on the attendees' knowledge of Manitoba's boreal forests. Some of the recommended revisions were scale-related, where FEC types were classified at a finer scale than CDC vegetation types, and two or more FEC types could be lumped together into a single CDC type. In other cases, the FEC appeared to miss out on forest types that are rare, obscure or that have no economic value.

Future challenges in Manitoba include incorporating parkland and riparian forests, as well as forested wetlands, into the FEC, and ensuring that planned

changes to the provincial forest land inventory are cross-walked to both the FEC and CDC classification.

Status and Applications of the International Classification of Ecological Communities in Ontario (Wasyl Bakowsky — Ontario Natural Heritage Information Centre)

The Ontario Natural Heritage Information Centre (NHIC) was established in the fall of 1993. To this day, there is no standardized provincial vegetation classification. Forests had previously been classified for the timber-producing portion of northern Ontario on a regional basis (Northwest Region: Sims et. al. 1989*; Northeast Region: McCarthy et al. 1994*), and Central Region was completed by 1997 (Chambers et al. 1997).

Since funding for the first two years of the NHIC came from Southern Region, initial work was focused on this area. At that time, the NHIC collaborated on a project with the Science and Technology Transfer Unit from that region, to develop a first approximation of an Ecological Land Classification (ELC) for southern Ontario. Little quantitative information existed for this area; consequently a community catalogue was developed to provide the basic framework and units of the ecological classification. Descriptions of documented vegetation communities were entered into a database, including dominant and associated species, soil data, and microclimate. The database was sorted by dominant species. Within a group of dominant species, similarities in soil moisture and type, associated species, etc. were used to further subdivide the groups into distinct vegetation types, with some of these separations based on subjective assessments.

Near the end of the cataloguing project, sufficient quantitative data existed and sufficient analysis of forested communities had been undertaken, so that this information was also used to refine the forest units. Consequently, the Southern Ontario ELC was published in 1998 (Lee et al. 1998).

Working with TNC's Midwest Regional Ecologist, the NHIC was able to produce conservation ranks for the 296 vegetation types listed for southern Ontario. Conservation ranks were also developed for the forest ecosystem classification forest types in northern Ontario. Additionally, as fieldwork and the collection of information expanded to northern Ontario, an ad-hoc list of community types not represented in regional classifications (e.g., non-forested types, or rare unrepresented types) was assembled and ranked as well.

Certain challenges exist with regard to a classification for Ontario. A comprehensive review is required to identify all vegetation types, particularly for non-forested communities. Because the scale and method of deriving forest types and vegetation types varies from region to region within the province, these need to be standardized.

Quebec Forest Ecosystem Classification (Vegetation Component) (Jean-Pierre Saucier — Forêt-Québec)

Forest Ecosystem Classification (FEC) by the Ministère des ressources naturelles du Québec started in 1986 (Saucier and Robert 1995; Bergeron et al. 1992). The FEC team is devoted to classifying major ecosystems by ecological regions, mapping ecosystems at different scales, and promoting the use of ecological classification in forest management (Robitaille and Saucier 1996; Bergeron et al. 1993). This work relies largely on 28 200 ecological sampling plots established specifically for this purpose (Saucier et al. 1994*).

To date, 10 ecological classification reports, which include keys for field recognition of forest types and ecological types, have been completed, and the last one is in progress (Gosselin et al. 1999; Grondin et al. 1998). A second team is dedicated to the identification and protection of exceptional ecosystems (old growth forest, rare ecosystems, habitat for rare or endangered species). Over 600 exceptional ecosystems have been located and described (Groupe de travail sur les écosystèmes forestiers exceptionnels 2000).

Forest ecosystem classification has led to a hierarchical system with 11 levels defined by the integration of ecological factors whose number, precision and heterogeneity vary among the different levels (Saucier et al., 1998*; Robitaille and Saucier 1998). The purpose is to describe the diversity and complexity of natural ecosystems from the local level to the global level. The nine higher levels (vegetation zone, subzone, bioclimatic domain, subdomain, ecological region, subregion, regional landscape unit, land district, and altitudinal vegetation level) are regionalizations, while the two lower levels (ecological type and forest type) are element based.

The forest types describe the present vegetation of a site. Forest types are based on physiognomy, forest cover composition and indicator species group of the understorey. Forest type is a floristic element based level and can be recognized directly from the vegetation present at a particular site.

The next level, ecological type, is a combination of potential vegetation (which expresses forest dynamics) and environmental features such as soil texture, moisture regime, landscape position or stoniness. This combination is considered permanent for a particular site under a certain climatic regime. While the number of forest types varies greatly within each bioclimatic subdomain, there are 190 distinct ecological types overall for the forested part of Québec. Ecological types are element based mapable units.

Le Ministère des ressources naturelles du Québec is willing to take part in a national vegetation classification project, and can provide a cross-walk between its forest types and associations or alliances. Despite the fact that it is purely vegetation based, the

national classification will be useful for Le Ministère's assessment of biodiversity GAP analysis and comparison with adjacent jurisdictions.

Vegetation Classification in Atlantic Canada (Sean Blaney — Atlantic Canada Conservation Data Centre)

The Atlantic Canada Conservation Data Centre (AC CDC) is the newest CDC in Canada (approximately three years since first hiring). [The Yukon CDC has since been created.] Much relevant information on the vegetation of the region is available [e.g., Hustich (1939, 1949); Loucks (1962); Damman (1963*, 1964, 1967); Bailey and Wellings (1981); Damman (1983); South (1983); Meades (1986); Meades and Moores (1989*); Zelazny et al. (1989a*, 1989b*); Meades and Roberts (1992); Sobey (1995*); Davis and Browne (1996); Wells (1996)]. A wide range of forest type classifications and ecoregional classifications have been developed, primarily by the provinces, but this information has generally been compiled for end uses and with methodologies that are different than those of the Canadian CDCs and neighbouring U.S. state natural heritage programs. The AC CDC has not made substantial progress in compiling existing information and developing a community classification system, due to the lack of capacity and the high initial priority of developing provincial conservation ranks and compiling Element Occurrence records for vascular plant taxa. The AC CDC will be hiring a full time ecologist who will systematically compile existing information and include partners in the process to help with eventual acceptance of the classification.

Approach to a Canadian Forest Ecosystem Classification (Bill Meades and Ken Baldwin — Canadian Forest Service)

The CFS is mandated to develop a forest ecosystem classification for Canada by:

- the Canadian Council of Forest Ministers criteria (Canadian Council of Forest Ministers 1997);
- the Forest Sector Strategy (Canadian Council of Forest Ministers 1998);
- the CFS's Strategic Plan (Natural Resources Canada 1998).

Rationale for development of a Canadian FEC includes:

- providing a national and international reporting framework for indicators of biodiversity conservation (Canadian Council of Forest Ministers 1997; Montreal Process Liaison Office 2000*);
- providing a standardized framework for assessment of forest health, sustainable development indicators, etc.
- providing an information framework for interrelating ecological information between local, regional, national, and international scales;
- providing a standardized reference nomenclature and ecological framework for spatial products at multiple scales;
- regional forest ecosystem classifications (FECs) in Canada have developed independently, so there is little correspondence between them; and,
- the level of redundancy among total regional FEC units is currently unknown.

The current objectives of the CFS are to:

- develop a first approximation national forest ecosystem classification with standardized nomenclature that:
  - describes variations of extant, mature forest community structure and species composition;
  - represents community variability in relation to environmental factors such as climate, soil fertility, moisture regime, aspect; and,
  - reflects originating conditions and stable temporal relationships (as much as possible);
- initiate the development of a national database of high quality forest ecology data that would support empirical validation of the proposed national FEC;
- develop a publication that documents the diversity of Canada's forest ecosystems in the context of the ecological processes that control their composition and distribution.

The CFS proposes to:

- adopt the ICEC as the classification standard for the Canadian national FEC;
- complete a reconnaissance cross-walk of regional FEC units through the ICEC to the formation level by August 2000, using published summary information (i.e., Quebec, Yukon, and coastal British Columbia; approximately 2500 FEC units from other provinces have already been completed);
- synthesize national floristic units (associations and alliances) by correlating published regional FEC units using the following criteria to assess ecological equivalency:
  - community physiognomy, floristics, dominance;
  - climatic regionalization;
  - site factors (fertility, moisture, aspect, etc.); and,
  - ecological process relationships (disturbance, successional phases, etc.);
- circulate draft national associations and alliances to regional/international ecologists for review; also seek comment on proposed matching of regional FEC types and U.S. alliances/associations to national units;
- sponsor regional meetings for revision of national associations/alliances and to confirm the matching of regional FEC types and U.S. alliances/associations to national units;
- develop descriptions of alliances and, depending on resources, associations (publication is not proposed within the 3-year time frame); and,
- using the intergovernmental Memorandum of Understanding process, initiate a request for forest ecology data from provincial/territorial governments and participate in the development of data standards for a national FEC database.

Proposal for a Canadian National Vegetation Classification (Don Faber-Langendoen — NatureServe)

Comparisons of classification systems in Canada (Ponomarenko et al. 2000*) indicate that the recently published ICEC (Grossman et al. 1998) could serve as the basis for establishing a CNVC. The ICEC is a physiognomic-floristic classification of existing vegetation with a strong emphasis on conservation and

resource management applications. It is, in part, a modification of an international physiognomic system developed for UNESCO by an international team of vegetation ecologists, with a hierarchical set of formation units. The ICEC also contains a nested set of floristic units (alliance and association) below the formation level that are compatible with other floristic classifications. Collaboration between NatureServe and the CDC program ecologists, in conjunction with other Canadian partners and the U.S. programs, would permit the development of a CNVC that would be part of a North America-wide effort.

Adoption of such a standard is not to suggest that the ICEC is fixed in stone. Rather, the CNVC would become part of an international process to ensure that the ICEC is more accurate in its classification of vegetation.

Decisions Made by the Group at the Workshop

- The ICEC should be the basis from which to develop a CNVC.
- A CNVC Working Group was established and consists of two sub-groups: a Steering Committee and a Science Committee.
- Serguei Ponamarenko should continue to coordinate all project components and serve as the secretary of the Working Group.
- A list of "drivers" of a CNVC was developed: State of the Environment reporting at the international, national and provincial/territorial/state levels; State of the Forest reporting; the Biodiversity Convention; Montreal Treaty criteria and indicators; GAP analysis for protected areas; ecoregional planning; ecosystem monitoring and indicators; park system plan — representation; State of the Parks reporting; climate change indicators; species management, including critical habitat for species at risk.

Progress Made Since the Workshop

The workshop was a turning point in crystallizing the network necessary to develop a Vegetation Classification Standard for Canada. In the fall of 2000, NatureServe-Canada was created to partner with NatureServe to manage the standardization of biodiversity information between Canada and the U.S., and to develop a national agenda for the Canadian Conservation Data Centres.

One of the major tasks for the new organization was to coordinate the development of the International Classification of Ecological Communities (ICEC), which up to this time has had a large US emphasis, with the development of the Canadian National Vegetation Classification (CNVC). Thus NatureServe-Canada, together with NatureServe and the Canadian Forest Service, developed a business plan and succeeded in obtaining funding from the Richard Ivey Foundation to allow the project to continue.

The CNVC Steering Committee is co-chaired by NatureServe-Canada Director Steve Curtis and CFS Director Bill Meades, while the CNVC Technical Committee is co-chaired by Ken Baldwin (CFS) and Don Faber-Langendoen (NatureServe). The Steering Committee oversees the direction of the whole initiative and provides strategic guidance, while the Technical Committee develops and implements common standards and processes, shares resources, and ensures that duplication does not occur among the various Canadian projects.

There are currently three projects going on within the initiative: (1) CFS is bringing the existing provincial and territorial forest ecosystem classifications under one national classification (this is the east-west correlation), (2) NatureServe is incorporating the CNVC into the ICEC (i.e., the north-south correlation), and (3) the Atlantic Canada CDC is developing a regional subset of the CNVC for the Maritime provinces by involving both the east-west and north-south correlations.

The CNVC will be just one way of describing Canada's ecosystems, so it will not necessarily be "the only correct way", if such a thing exists. Its main contributions will be its role as a national standard and its place within an international standard.

After the first few years since the outset of the project, it seems safe to conclude that there is a general recognition of the need for a CNVC, not only by ecologists but also by provincial and federal governments. People agree that the ICEC should serve as the starting point, this being due in large part not only to the fact that its design is logical, but also to the fact that it is still under development and that the cooperators (in the U.S., in some Latin American countries, and in Canada) are contributing directly to its development. Finally, there has been excellent cooperation among the numerous ecologists in Canada and the U.S. The main challenge is to obtain funding for the project over the long term, because after the initial classification is developed over the next few years (additional monies are required even for this to happen), the classification will have to be updated continually. For further information, see the website: www.glfc.cfs.nrcan.gc.ca/CFEC and www.natureserve.org/explorer.

Acknowledgments

We thank all those who participated in the workshop and those who subsequently joined either the Steering Committee or the Technical Committee. We also thank Don Faber-Langendoen, Ken Baldwin, the late Antoni Damman, and two anonymous readers for reviewing this manuscript. Bob Manson read the galley proofs. Parks Canada kindly held the workshop and covered the publication costs and reprint charges for this paper. The workshop would not have happened without the initial suggestion by Dennis Grossman or without the support at all stages of its preparation from Nik Lopoukhine.

Documents Cited

Achuff, P. L., W. D. Holland, G. M. Coen, and **K. Van Tighem.** 1984a. Ecological land classification of Kootenay National Park, British Columbia. Volume I: Integrated resource description. Alberta Institute of Pedology Publication M-84-10: 373 pages + maps.

Achuff, P. L., W. D. Holland, G. M. Coen, and **K. Van Tighem.** 1984b. Ecological Land Classification of Mount Revelstoke and Glacier National Parks, British Columbia. Volume I: Integrated resource description. Alberta Institute of Pedology Publication M-84-11: 261 pages + maps.

Achuff, P. L., R. L. McNeil, and **M. L. Coleman.** 1997a. Ecological land classification of Waterton Lakes National Park, Alberta. Parks Canada, Waterton Lakes National Park. 250 pages + maps.

Achuff, P. L., W. S. Taylor, L. J. Knapik, C. Wallis, C. Wershler, and **J. Salt.** 1997b. Ecological land classification of Yoho National Park, British Columbia. Volume 1: Integrated resource description. Parks Canada, Yoho National Park, Field, British Columbia. 383 pages + maps.

Agriculture and Agri-Foods Canada. 1998. Soil Landscapes of Canada, Version 2.2 and Organic Carbon Digital Database of Canada.

Bakowsky, W. D. 1996. Natural heritage resources of Ontario: Vegetation communities of southern Ontario. Ontario Ministry of Natural Resources, Natural Heritage Information Centre, Peterborough, Ontario. 19 pages.

Belcher, J. 1994. Saskatchewan community classification — terrestrial grasslands (preliminary draft). Saskatchewan Conservation Data Centre, Regina, Saskatchewan. 15 pages.

British Columbia Conservation Data Centre. 1996. Provincial tracking list for plant communities. Resource Inventory Branch, Ministry of Environment, Lands and Parks, Victoria, British Columbia. 19 pages.

Canadian Forest Service. 2000. A plot-based national forest inventory design for Canada. Document Version 3.1. 140 pages.

Comer, P. (*Editor*), **L. Allen, S. Cooper, D. Faber-Langendoen,** and **G. Jones.** 1999. Selected shrubland and grassland communities of the northern Great Plains. The Nature Conservancy. 119 pages.

Damman, A. W. H. 1963. A reconnaissance survey of the ecological conditions in the forest of the Roddicton area, Newfoundland. Canada Department of Forestry. Mimeo 63-N-1. 101 pages.

Ecological Stratification Working Group. 1995. A national ecological framework for Canada. Agriculture and Agri-Food Branch, Ottawa/Hull. Report and national map at 1:7,500,000 scale. 125 pages.

Epp, H., and **S. Matthews.** 1998. Habitat/vegetation classification for the West Kitikmeot/Slave Study Region. Annual Report submitted to West Kitikmeot/Slave Study Society. 18 pages + figures.

Greenall, J. A. 1996. Manitoba's terrestrial plant communities. Manitoba Conservation Data Centre, MS Report Number 96-02. 32 pages.

Kennedy, C. E., C. A. S. Smith, D. Cooley, S. Kokelj, and **C. Burn.** 2000. Environmental Monitoring on Herschel Island, Yukon. Poster presented at the 51st Arctic Science Conference, Whitehorse, Yukon; September 21–24, 2000; American Association for the Advancement of Science and the Yukon Science Institute.

McCarthy, T. G., R. W. Arnup, J. Nieppola, B. G. Merchant, K. C. Taylor, and **W. J. Parton.** 1994. Field guide to forest ecosystems of northeastern Ontario. Ontario Ministry of Natural Resources, Northeast Science and Technology. NEST Field Guide FG-001.

Meades, W. J., and **L. Moores.** 1989. Forest site classification manual: a field guide to the Damman forest types of Newfoundland. Natural Resources Canada, Canadian Forest Service and Newfoundland Department of Forestry and Agriculture, FRDA Report 003.

Montreal Process Liaison Office. 2000. The Montreal Process: Year 2000 Progress Report. Progress and innovation in implementing criteria and indicators for the conservation and sustainable management of temperate and boreal forests. Montreal Process Liaison Office, Natural Resources Canada, Canadian Forest Service, Ottawa, Ontario. 97 pages.

National Vegetation Working Group. 1990. The Canadian vegetation classification system — first approximation. Canadian Committee on Ecological Land Classification. *Edited by* W.L. Strong, E.T. Oswald and D.J. Downing. Ecological Land Classfication Series No. 25. Sustainable Development, Corporate Policy Group, Environment. Ottawa. 22 pages.

Oosenbrug, S., and **E. Gah.** 1998. Using representative landscape units to help establish a network of protected natural areas in the Northwest Territories. Background paper for the Northwest Territories Protected Areas Strategy, Department of Resources, Wildlife and Economic Development. 10 pages.

Oswald, E. T., and **J. P. Senyk.** 1977. Ecoregions of Yukon Territory. Fish and Environment Canada. Canadian Forestry Service, Pacific Forest Research Centre , Information Report CC-X-164. 115 pages.

Ponomarenko, S., R. Alvo, K. Baldwin, D. Faber-Langendoen, D. Grossman, O. Hendrickson, K. Maybury, N. Lopoukhine, and **D. Welch.** 2000. Developing a Canadian National Vegetation Classification. Parks Canada. Hull, Quebec. 32 pages.

Saucier, J.-P., J.-P. Berger, H. D'avignon, and **P. Racine.** 1994. Le point d'observation écologique, normes techniques. Gouvernement du Québec, Ministère des Ressources Naturelles, Service des inventaires forestiers, Québec. 116 pages.

Saucier, J.-P., J.-F. Bergeron, P. Grondin, and **A. Robitaille.** 1998. Les régions écologiques du Québec méridional: un des éléments du système hiérarchique de classification écologique du territoire mis au point par le ministère des Ressources naturelles. L'Aubelle, février-mars 1998. 8 pages.

Sims, R. A., W. D. Towill, K. A. Baldwin, and **G. M. Wickware.** 1989. Forest ecosystem classification for northwestern Ontario. Ontario Ministry of Natural Resources, Northwestern Ontario Forest Technology Development Unit, Technical Report. Thunder Bay, Ontario. 191 pages.

Sobey, D. G. 1995. Analysis of the ground flora and other data collected during the 1991 Prince Edward Island Forest Inventory, II. Plant community analysis. PEI Forestry Division, Department of Agriculture, Fisheries and Forestry, Charlottetown, PEI, Canada. 167 pages.

Thiesenhausen, K., and **A. Veitch.** 1998. Vegetation Classification Project, Sahtu Settlement Area. Summary of the 1998 Field Season. Department of Resources, Wildlife and Economic Development, Government of the Northwest Territories. 7 pages + attachments.

Viereck, L. A., and **L. A. Schandelmeier.** 1980. Effects of fire in Alaska and adjacent Canada — a literature review. Technical Report 6. US Department of the Interior, Bureau of Land Management, State Office. Anchorage, Alaska. 124 pages.

Zelazny, V. F., T. T. M. Ng, M. G. Hayter, C. L. Bowling, and **D. A. Bewick.** 1989a. Field guide to forest site classification in New Brunswick, Big Bald-Sevogle site regions. New Brunswick Department of Natural Resources and Energy. 43 pages.

Zelazny, V. F., T. T. M. Ng, M. G. Hayter, C. L. Bowling, and **D. A. Bewick.** 1989b. Field guide to forest site classification in New Brunswick, Harvey - Harcourt/Fundy site regions. New Brunswick Department of Natural Resources and Energy. 43 pages.

Zimmer, A., L. Robinson, A. Veitch, R. Trembath, and **N. Whiteman.** 1999. Sahtu Settlement Area Vegetation Classification. Project Progress Report — 1999. Department of Resources, Wildlife and Economic Development, Government of the Northwest Territories. 24 pages.

Literature Cited

Anderson, M., P. Bourgeron, M. T. Bryer, R. Crawford, L. Engelking, D. Faber-Langendoen, M. Gallyoun, K. Goodin, D. H. Grossman, S. Landaal, K. Metzler, K. D. Patterson, M. Pyne, M. Reid, L. Sneddon, and **A. S. Weakley.** 1998. Terrestrial vegetation of the United States. Volume II: List of vegetation types. The Nature Conservancy, Arlington, Virginia.

Anderson, M., P. Comer, D. Grossman, C. Groves, K. Poiani, M. Reid, R. Schneider, B. Vickery, and **A. Weakley.** 1999. Guidelines for representing ecological communities in ecoregional conservation plans. The Nature Conservancy, Arlington, Virginia. 74 pages.

Bailey, R. E., and **F. R. Wellings.** 1981. Forest species associations in Nova Scotia. Nova Scotia Department of Lands and Forests. 9 pages.

Beckingham, J. D., and **J. H. Archibald.** 1996. Field guide to ecosites of Northern Alberta. Natural Resources Canada, Canadian Forest Service. Northern Forestry Centre, Edmonton, Alberta. Special Report 5.

Beckingham, J. D., I. G. W. Corns, and **J. H. Archibald.** 1996a. Field guide to ecosites of West-central Alberta. Natural Resources Canada, Canadian Forest Service. Northern Forestry Centre, Edmonton, Alberta. Special Report 9.

Beckingham, J. D., D. G. Nielson, and **V. A. Futoransky.** 1996b. Field guide to ecosites of the mid-boreal upland ecoregions of Saskatchewan. Natural Resources Canada, Canadian Forest Service. Northwest Region, Northern Forestry Centre, Edmonton, Alberta. Special Report 6.

Bell, M. A. M. 1964. Phytocoenoses in the dry subzone of the interior western hemlock zone of British Columbia. Ph.D. thesis, Department of Biology and Botany, University of British Columbia, Vancouver. 246 pages.

Bergeron, J.-F., J.-P. Saucier, A. Robitaille, P. Grondin, and **D. Robert.** 1993. The Québec forest ecological survey program, a set of tools for sustainable forest management. Conférence présentée au congrès de l'International Union of Forest Research Organisations: Advancement in Forest Inventory and Forest Management Science, Séoul, Corée du sud. 17 pages.

Bergeron, J.-F., J.-P. Saucier, A. Robitaille, and **D. Robert.** 1992. Québec forest ecological classification program. Forestry Chronicle 68: 53-63.

Biodiversity Convention Office. 1995. Canadian Biodiversity Strategy: Canada's Response to the Convention on Biological Diversity. 80 pages.

Braun-Blanquet, J. 1928. Pflanzensoziologie. Grundzuge der vegetationskunde. Springer-Verlag, Berlin, Germany.

Brooke, R. C. 1966. Vegetation-environment relationships of sub-alpine mountain hemlock zone ecosystems. Ph.D. thesis, Department of Biology and Botany, University of British Columbia, Vancouver. 330 pages.

Canadian Council of Forest Ministers. 1997. Criteria and indicators of sustainable forest Management in Canada. Canadian Council of Forest Ministers, Ottawa, Ontario. 47 pages.

Canadian Council of Forest Ministers. 1998. National forest strategy: 1998–2003. Canadian Council of Forest Ministers, Ottawa, Ontario. 47 pages. http://nfc.forest.ca

Ceska, A. 1979. Vegetation classification: I. A computer program for handling vegetation data; II. Wetland plant communities in the wet Douglas fir subzone on Vancouver Island. xii + 234 pages.

Chambers, B. A., B. J. Naylor, J. Nieppola, B. Merchant, and **P. Uhlig.** 1997. Field guide to forest ecosystems of central Ontario. Ontario Ministry of Natural Resources, Southcentral Science Section, Science Development and Transfer Branch. SCSS Field Guide FG-01. 200 pages.

Clement, C. J. 1981. Vegetation resources of the Vernon map sheet area. 2 Volumes. British Columbia Ministry of the Environment, Assessment and Planning Division Bulletin 19. Kelowna, British Columbia.

Damman, A. W. H. 1964. Some forest types of central Newfoundland and their relationship to environmental factors. Forest Science Monograph Number 8. 62 pages.

Damman, A. W. H. 1967. The forest vegetation of western Newfoundland and site degradation associated with vegetation change. Ph.D. thesis, University of Michigan, Ann Arbor. 319 pages.

Damman, A. W. H. 1983. An ecological subdivision of the island of Newfoundland. Monographiae Biologicae 48: 163–206.

Dansereau, P. 1959. Phytogeographia Laurentiana. I. The principal plant associations of the Saint-Lawrence Valley. Institut de Botanique de l'Université de Montréal. Contribution 75. 145 pages.

Davis, D. S., and **S. Browne.** *Editors.* 1996. The natural history of Nova Scotia. Volume 1, Topics and habitats. Revised edition. Nova Scotia Museum. 518 pages.

Ecological Stratification Working Group. 1993. Ecoregions of Canada. Agriculture Canada, Research Branch, Centre of Land Biology Research, Environment Canada, State of the Environment Report, Ottawa, Ontario.

Gosselin, J., P. Grondin, and **J.-P Saucier.** 1999. Rapport de classification écologique du sous-domaine bioclimatique de l'érablière à bouleau jaune de l'ouest. Gouvernement du Québec, Ministère des Ressources Naturelles, Direction des inventaires forestiers, Québec, 186 pages.

Grandtner, M. M., and **F. Vaucamps.** 1982. Vegetation science and forestry in Canada. Pages 15–45 in Handbook of vegetation science, Part 12. *Edited by* G. Jahn. Dr. W. Junk Publishers, The Hague, Netherlands.

Green, R. N., and **K. Klinka.** 1994. A field guide to site identification and interpretation for the Vancouver Forest Region. Research Branch, British Columbia Ministry of Forests, Land Management. Handbook Number 28. 285 pages.

Grondin, P., J. Blouin, and **P. Racine.** 1998. Rapport de classification écologique du sous-domaine bioclimatique de la sapinière à bouleau blanc de l'ouest. Gouvernement du Québec, Ministère des Ressources Naturelles, Direction des inventaires forestiers, Québec. 220 pages.

Grossman, D. H., D. Faber-Langendoen, A. S. Weakley, M. Anderson, P. Bourgeron, R. Crawford, K. Goodin, S. Landaal, K. Metzler, K. D. Patterson, M. Pyne, M. Reid, and **L. Sneddon.** 1998. International classification of ecological communities: terrestrial vegetation of the United States. Volume 1. The National Vegetation Classification System: development, status and applications. The Nature Conservancy, Arlington, Virginia, USA. 126 pages.

Groupe de travail sur les écosystèmes forestiers exceptionnels. 2000. Les écosystèmes forestiers exceptionnels du Québec: bilan des travaux réalisés 1997–2000. Rapport d'étape. Gouvernement du Québec, Ministère des Ressources Naturelles, Direction de l'environnement forestiers, Québec. 47 pages.

Halliday, W. E. D. 1937. A Forest Classification for Canada. Forest Service Bulletin 89. Canada, Department of Mines and Resources.

Holland, W. D., and **G. M. Coen.** *Editors.* 1982. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume II: Soil and vegetation resources. Alberta Institute of Pedology Publication SS-82-44: 540 pages + maps.

Hunter, M. 1991. Coping with ignorance: the coarse-filter strategy for maintaining biodiversity. Pages 256–281 *in* Balancing on the Brink of Extinction: the Endangered Species Act and Lessons for the Future. *Edited by* K. A. Kohm, Island Press, Washington, D.C.

Hustich, I. 1939. Notes on the coniferous forest and tree limit on the east coast of Newfoundland-Labrador. Acta Geographica 7(1): 1–77.

Hustich, I. 1949. On the forest geography of the Labrador Peninsula. A preliminary synthesis. Acta Geographica 10(2): 1–63.

Jenkins, R. E. 1976. Maintenance of natural diversity: approach and recommendations. Pages 441–451 *in* Transactions of the 41st North American Wildlife Conference, 4 March 1976, Washington, D.C. Wildlife Management Institute, Washington, D.C.

Klinka, K., H. Qian, J. Pojar, and **D. V. Meidinger.** 1996. Classification of natural forest communities of coastal British Columbia, Canada. Vegetation 125: 149–168.

Krajina, V. J. 1959. Biogeoclimatic zones in British Columbia. University of British Columbia, Botanical Series 1: 1–47.

Krajina, V. J. 1960. Can we find a common platform for the different schools of forest type classifications? Sylva Fennica 105: 50–55.

Krajina, V. J. 1965. Biogeoclimatic zones and biogeocoenoses of British Columbia. Ecology of Western North America 1: 1–17.

Krajina, V. J. 1969. Ecology of forest trees in British Columbia. Ecology of Western North America 2: 1–146.

Krestov, P., K. Klinka, C. Chourmouzis, and **C. Hanel.** 2000a. Classification of trembling aspen ecosystems in British Columbia. Forest Sciences Department, University of British Columbia, Vancouver. Scientica Silvica Extension Series, Number 27. 112 pages.

Krestov, P. K. Klinka, C. Chourmouzis, and **G. Kayahara.** 2000b. Classification of mid-seral black spruce ecosystems of northern British Columbia. Forest Sciences Department, University of British Columbia, Vancouver. Scientica Silvica Extension Series, Number 26. 102 pages.

Lea, E. C. 1984. Biophysical resources of the East Kootenay area: vegetation. British Columbia Ministry of the Environment, Ministry of the Environment Technical Report Number 5. Kelowna, British Columbia.

Lee, H., W. Bakowsky, J. Riley, J. Bowles, M. Puddister, P. Uhlig, and **S. McMurray.** 1998. Ecological land classification for southern Ontario: first approximation and its application. Ontario Ministry of Natural Resources, Southcentral Science Section, Science Development and Transfer Branch. SCSS Field Guide FG-02. 225 pages.

Loucks, O. L. 1962. A forest classification for the Maritime provinces. Proceedings of the Nova Scotia Institute of Science. Volume 25 Part 2: 86–184.

MacKinnon, A., D. Meidinger, and **K. Klinka.** 1992. Use of the biogeoclimatic ecosystem classification system in British Columbia. Forestry Chronicle 68: 100–120.

Maybury, K. P. 1999. Seeing the forest and the trees: ecological classification for conservation. The Nature Conservancy, Arlington, Virginia. 37 pages.

McAllister, D. E. 2000. A hierarchical marine ecosystem classification completed for Canada's West Coast. Sea Wind 14: 4–6.

McLean, A. 1970. Plant communities of the Similkameen Valley, British Columbia, and their relationships to soils. Ecological Monographs 40: 403–424.

Meades, W. J. 1986. Successional status of ericaceous dwarfshrub heath in eastern Newfoundland. Ph.D. thesis, University of Connecticut. 355 pages.

Meades, W. J., and **B. A. Roberts.** 1992. A review of forest site classification activities in Newfoundland and Labrador. The Forestry Chronicle 68: 25–33.

Meidinger, D., and **J. Pojar.** *Compilers and editors.* 1991. Ecosystems of British Columbia. British Columbia Ministry of Forests, Special Report Series Number 6. 330 pages.

Moss, E. H. 1932. The vegetation of Alberta IV: The poplar association and related vegetation of central Alberta. Journal of Ecology 20: 380–415.

Moss, E. H. 1944. The Prairie and associated vegetation of southwestern Alberta. Canadian Journal of Research. Volume 22, Section C., 11–31.

Moss, E. H. 1952. Grassland of the Peace River Region, Western Canada. Canadian Journal of Botany 30: 98–124.

Moss, E. H. 1953. Marsh and bog vegetation in northwestern Alberta. Canadian Journal of Botany 31: 448–470.

Moss, E. H. 1955. The vegetation of Alberta. The Botanical Review 21, November 1955, No. 9.

Moss, E. H., and **J. A. Campbell.** 1947. The fescue grassland of Alberta. Canadian Journal of Research 25, Section C.

National Wetlands Working Group. 1987. The Canadian Wetland Classification System. Ecological Land Classification Series, Number 21. Sustainable Development Branch, Environment Canada. Ottawa, Ontario. 14 pages.

Natural Resources Canada. 1998. Canadian Forest Service strategic plan: beyond the millenium 1998– 2003. Canadian Forest Service, Ottawa, Ontario. 18 pages.

Orloci, L. 1961. Forest types of the coastal western hemlock zone. M.Sc. thesis, Department of Biology and Botany, University of British Columbia, Vancouver. 206 pages.

Peterson, E. B. 1964. Plant associations in the subalpine mountain hemlock zone in southern British Columbia. Ph.D. thesis, Department of Biology and Botany, University of British Columbia, Vancouver. 171 pages.

Pojar, J., K. Klinka, and **D. V. Meidinger.** 1987. Biogeoclimatic ecosystem classification in British Columbia. Forest Ecology Management 22: 119–154.

Ponomarenko, S., and **R. Alvo.** 2000. Perspectives on developing a Canadian classification of ecological communities. Canadian Forest Service, Information Report ST-X-18E, Ottawa. 50 pages.

Raup, H. M. 1928. A survey of the vegetation of Shelter Point, Athabasca Lake. University of Pittsburgh. Pittsburgh, Pennsylvania. 53 pages.

Raup, H. M. 1935. Botanical Investigations in Wood Buffalo Park. Bulletin Number 74, Biological Series, Number 20. Canada Department of Mines and National Museum of Canada. Ottawa, Ontario. 174 pages.

Revel, R. 1972. Phytocoenoses of the Sub-Boreal Spruce Biogeoclimatic Zone in north central British Columbia. Ph.D. thesis, Department of Botany, University of British Columbia, Vancouver. 410 pages.

Robitaille, A., and **J.-P. Saucier.** 1996. Land districts, ecophysiographic units and area: the landscape mapping of the Ministère des Ressources Naturelles du Québec. Environmental Monitoring and Assessment 39: 127–148.

Robitaille, A., and **J.-P Saucier.** 1998. Les paysages régionaux du Québec méridional. Les publications du Québec, Québec. 213 pages.

Roemer, H. L. 1972. Forest vegetation and environments on the Saanich Peninsula, Vancouver Island. Ph.D. thesis, Department of Biology, University of Victoria, Victoria, British Columbia. 405 pages.

Rowe, J. S. 1959. Forest regions of Canada. Department of Northern Affairs and National Resources, Forestry Branch, Bulletin 123.

Saucier, J.-P., and **D. Robert.** 1995. Présentation du programme de connaissance des écosystèmes forestiers du Ministère des Ressources Naturelles du Québec. Revue forestière française 47(1): 71–74.

South, G. R. *Editor.* 1983. Biogeography and ecology of the island of Newfoundland. Dr W. Junk Publishers, The Hague, Netherlands. 723 pages.

Stein, B. A., L. S. Kutner, and **J. S. Adams.** 2000. Precious heritage: the status of biodiversity in the United States. Oxford University Press, New York (New York). 399 pages.

Tisdale, E. W. 1947. The grasslands of the southern interior of British Columbia. Ecology 28: 346–382.

UNESCO. 1973. International classification and mapping of vegetation, Series 6, Ecology and Conservation. United Nations Educational, Scientific, and Cultural Organization. Paris. 93 pages.

Van Ryswyk, A. L., A. McLean, and **L. S. Marchand.** 1966. The climate, native vegetation, and soils of some grasslands at different elevations in British Columbia. Canadian Journal of Plant Science 46: 35–50.

Wells, D. E. 1996. Classification of peatland vegetation in Atlantic Canada. Journal of Vegetation Science 7: 847–878.

Westhoff, V., and **E. van der Maarel.** 1978. The Braun–Blanquet approach. Pages 289–374 *in* Classification of plant communities. *Edited by* R. H. Whittaker. Dr. W. Junk, The Hague, Netherlands.

Whitford, H. N., and **R. D. Craig.** 1918. Forests of British Columbia. Commission of Conservation Canada, Committee on Forests, Ottawa, Ontario. 409 pages + maps.

Wiken, E. B., D. M. Welch, G. R. Ironside, and **D. G. Taylor.** 1981. The northern Yukon: an ecological land survey. Environment Canada, Ecological Land Classification Series Number 6. 197 pages, 2 maps.

Zoladeski, C. A., D. W. Cowell, and **Ecosystem Classification Advisory Committee.** 1996. Ecosystem classification for the southeast Yukon: field guide, first approximation. Yukon Renewable Resources, Canadian Forest Service, Department of Indian Affairs and Northern Development, Whitehorse, Yukon. 409 pages.

Zoladeski, C. A., G. M. Wickware, R. J. Delorme, R. A. Sims, and **I. G. W. Corns.** 1995. Forest ecosystem classification for Manitoba: field guide. Natural Resources Canada, Canadian Forest Service, Northwest Region, Northern Forest Centre, Edmonton, Alberta. Special Report #2. 205 pages.

Received 10 November 2000
Accepted 19 January 2002

A Tribute to William Earl Godfrey, 1910–2002

MICHEL GOSSELIN[1], EDWARD L. BOUSFIELD[2], AND STEWART D. MACDONALD[3]

[1]Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, Ontario K1P 6P4 Canada
[2]1710-1275 Richmond Road, Ottawa, Ontario K2B 8E3 Canada
[3]580 Thomas Dolan Parkway (Dunrobin), Ottawa, Ontario K0A 1T0 Canada

Gosselin, Michel, Edward L. Bousfield, and Stewart D. MacDonald. 2003. A tribute to William Earl Godfrey, 1910–2002. Canadian Field-Naturalist 117(1): 140–150.

Earl Godfrey, one of the most influential professionals in recent Canadian ornithology, was born in Wolfville, Nova Scotia, on 18 March 1910 and died in Ottawa on 8 June 2002. It is usual to acknowledge the passing of such a leading figure as the "end of an era", but such is not the case with Earl. Far from being the man of a single era, he was riding smoothly through time as a sort of intemporal figure, current and relevant until the end. Earl was born in the days when the Passenger Pigeon was still extant and when horses were pulling cartloads of sandstone blocks across the dusty outskirts of Ottawa in order to finish a new museum dedicated to the memory of Queen Victoria. In contrast, in the weeks preceding his admission to hospital, he was driving the Ottawa Queensway (named after the great-grand-daughter of Queen Victoria) in his 2002 Toyota Camry, and he was in touch with fellow ornithologists world-wide via e-mail and the internet.

Earl often recounted how a boyhood meeting with Robie Tufts, Chief Migratory Birds Officer for the Maritime Provinces, triggered his ever-lasting interest in birds[1]. With the guiding hand of Tufts never far behind, Earl earned a B.Sc. at Acadia University in 1934, in the midst of the Great Depression, and was able to do contract work for the National Museum of Canada in the summer of 1935 (Cape Breton Island) and again in 1939 (New Brunswick). In 1939, on the recommendation of Tufts, he was hired as tutor for the son of Cyrus Eaton, a Nova Scotia-born industrialist residing in Cleveland, Ohio, and one of the founders of the Cleveland Museum of Natural History. Earl always talked with fondness of his years in Cleveland and of all the tennis he was able to play when residing with the Eatons. He managed to attend graduate school at the Western Reserve University in 1939 and 1940 before moving on to do war-related work at the General Electric product development laboratory in Cleveland. During that period, he was also working as an unpaid curatorial assistant at the Cleveland Museum of Natural History, where Harry C. Oberholser, a legendary figure in American ornithology, was the Curator of Birds[2]. In 1942, when Oberholser was away from the Cleveland Museum to do contract work for the U.S. Biological Survey, Earl became Acting Curator. Earl met and married his first wife, Jane Vivian, in Cleveland, and his only daughter, Barbara, was born there. Earl and Jane were divorced in 1955.

Early in 1947, the Acting Chief of both the Biological and Ornithological Divisions at the National Museum of Canada, Austin Rand, was planning to leave his position in order to join the Field Museum of Natural History in Chicago[3]. Rand, himself a Wolfville protégé of Tufts, hired Earl as zoologist in charge of the ornithology unit at the National Museum. It was in the spring of 1947 that Earl accompanied Austin Rand for a short visit to the home of Percy Taverner. Taverner died a few weeks later, and this was therefore the only meeting between Godfrey and Taverner, two men who, between them, have dominated ornithology in Canada for most of the 20th century[4].

At the National Museum

On his arrival at the National Museum, Earl Godfrey immediately made plans to publish an entirely new volume on the birds of Canada. To this end, he embarked on a carefully coordinated series of field expeditions to regions of the country that were not well represented in the Museum's bird collection. During the next 30 years, Earl conducted or commissioned field studies in every province and territory to fill these ornithological gaps (see Appendix 1). His personal field investigations were concentrated in the Prairies, the interior of British Columbia, and around the Gulf of St. Lawrence. These expeditions were usually the topic of comprehensive taxonomic reports in the Bulletins of the National Museum (see Appendix 2).

Over that period, Earl was most capably assisted by no less than 25 different assistants, of whom eight were permanent museum staff members, and the others recruited mainly from universities. His assistants were uniform in their praise of Earl's great natural sensitivity to birds and their environment, of his supreme skill as a field biologist, and of his friendly attitude towards people. Hard-working himself, he expected and got in response similar dedication from others. His principal assistant was SDM, who later became the museum's Curator of Vertebrate

W. Earl Godfrey in the field at Lake Mistassini, Quebec, in 1947. (Reproduced courtesy of Canadian Museum of Nature).

Ethology (1966) and who single-handedly filled in many of the ornithological gaps in the Canadian High Arctic (see Appendix 1). Another was Henri Ouellet, Assistant Curator of Birds (1970-1976), who assumed dual roles as Head of the Vertebrate Zoology Division and Curator of Ornithology, upon Earl's retirement from these positions in 1976[5].

In the realm of public relations, Earl was always intensely interested in observations by bird-watchers of all levels, and he spent many office hours listening to, noting down, and commenting upon what they had to say. Earl's dedication meant that he often worked in his office late into the evening, making up for research time lost responding to public inquiries during the day.

In addition to museum work, Earl actively studied the birds around Ottawa, and, for years, many of his observations were recorded in the weekly columns of John Bird, in the *Ottawa Journal*, and Wilf Bell, in the *Ottawa Citizen*. He also contributed very significantly to Ottawa Field-Naturalists' Club bird counts, often in the company of his loyal friend and botanical compatriot Doug Savile, and earlier with Club members Fred Bourguignon and Rowley Frith[6]. After he moved to Nepean [now west-end Ottawa] in 1970, Earl entered his observations in a daily journal. His "backyard list" rose to 148 species, and, in the fall of 2001, shortly before being admitted to

W. Earl Godfrey at work on the fourth floor of the Victoria Memorial Museum Building in Ottawa in 1953. (Reproduced courtesy of Canadian Museum of Nature, J2036B).

hospital for circulatory problems, he was still surveying favourite areas along the Ottawa River.

A side not well known to ornithologists was that Earl was quite a sports enthusiast. He was an ardent fan of the Ottawa Rough Riders football team, from his arrival in Ottawa until the team's demise, and the new Ottawa Senators hockey team, from its founding. ELB remembers a trip with Earl, towing a little Shasta trailer to Alfred (60 km east of Ottawa) one gorgeous Saturday in the mid-1950s. There they ran an outside antenna for the portable television set and watched in frustration the "snowy" figures of the Rough Riders battling it out with the Alouettes in Montreal, a game unavailable on the Ottawa TV channel.

Earl's constant liaison with National Museum colleagues and support staff included regular gatherings of the Zoology Division "12:15 Luncheon Club". In the early 1950s, in addition to Earl and ELB, regular participants included mammalogist Austin Cameron, museum clerk Vi Humphreys[7], and secretaries Jean Cameron (Austin's sister), Vera Atkinson, and Mary Murphy, as well as botanist Bill Baldwin[8]. A ping-pong table, supposedly for all staff, was used 99% of the time by only two, Earl and ELB, who, during the following 35 years of noon-hour use, may well have played 40 000 individual games. When shots were missed, or the opponent became a bit lucky with impossible-to-return "edgers" and "roll-overs", the language was a bit picturesque.

After his marriage to Marilyn Legge in 1970 and his formal museum retirement in 1977, Earl became an ever more gracious and generous host. He and his wife frequently entertained guests at their home on Sioux Crescent. With Marilyn, the topic of conversation was usually politics and her work with the Humane Society of Ottawa-Carleton. With Earl, increasingly during the 1980s, discussions focused on the loss of museum research staff, the shutting down of museum research publications, and the rapidly increasing size of the National Museum of Natural Sciences' bureaucracy. Following the death of Marilyn in 1987, Earl continued to be a gracious host. He was most fortunate in his selection of dedicated and thoughtful housekeepers, all fine cooks.

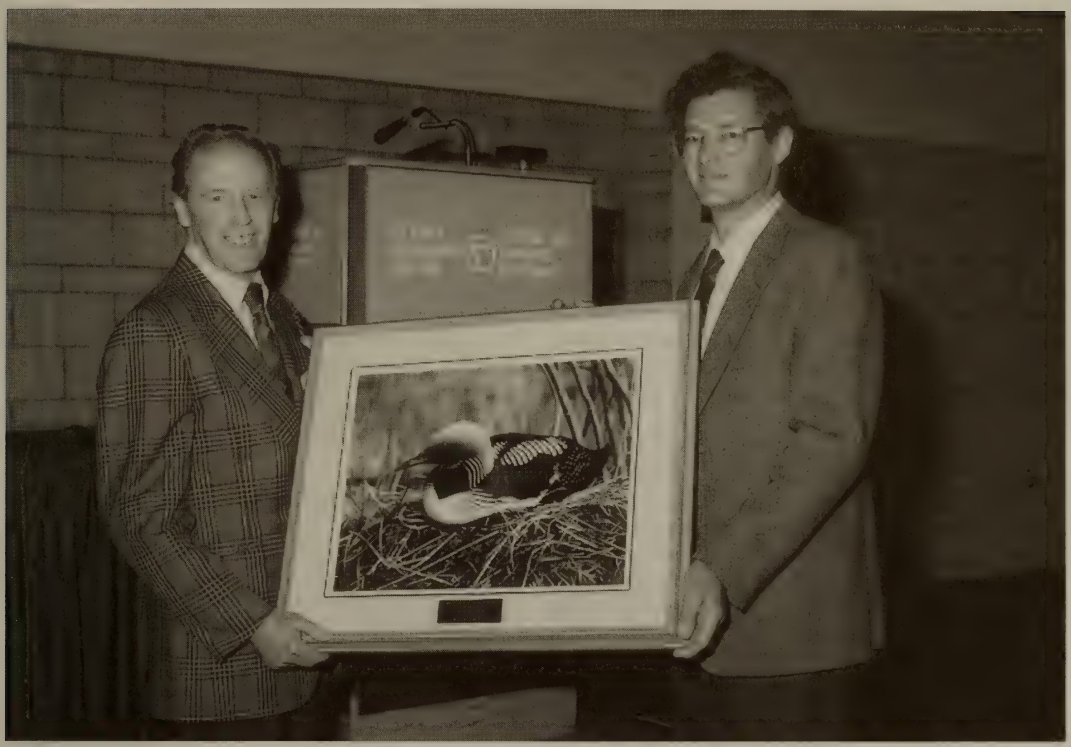
Endeavours and Publications

Earl Godfrey's magnum opus is unquestionably *The Birds of Canada*. First issued in 1966 and completely revised in 1986, this publication set new standards against which ornithological handbooks were later to be judged. Among its innovations were coloured range maps for almost every breeding species, and colour plates that group birds in the Peterson field-guide fashion (instead of the decorative portraits that adorned handbooks up to then). The plates are the work of John Crosby, a museum staff artist whose talent for depicting subtle details was a perfect match for Earl's high standards. Such book features may now be taken for granted, but a glance at library shelves will compel anyone to acknowledge that handbooks published before *The Birds of Canada* belong to another era and that handbooks published since (e.g., *The Birds of the Western Palaearctic*, *The Birds of Africa*, and the *Handbook of Australian, New Zealand, and Antarctic Birds*) have adopted strikingly similar formats, down to the colour of the maps. One feature remains unique to *The Birds of Canada*: its success in gathering as much information as possible in a single, fair-priced volume that appeals to the lay public as well as the professionals — the book's combined sales figures of nearly 300 000 copies for the successive French- and English-language editions attest to its continuing excellence.

Much of the distributional information included in *The Birds of Canada* is the product of the museum's ornithological expeditions, but perhaps even more important than these field trips were the data amassed by means of correspondence with hundreds of observers across the country. This massive amount of information was compiled in a system of index cards and maps created by Taverner in 1912 and updated throughout Earl's tenure with the help of museum registrar Vi Humphreys. Needless to say, Earl was appalled when the museum management discontinued this data-gathering effort following Vi's death in 1984.

Earl's fastidious attention to proper wording, correct grammar, and clear concepts made him a

W. Earl Godfrey (left) and A. W. Frank Banfield examine a specimen of Labrador Duck in 1968. (Reproduced courtesy of Canadian Museum of Nature, Photo number J19936-1).



W. Earl Godfrey (left) receives the first Doris Heustis Speirs Award from the Society of Canadian Ornithologists, presented to him by Spencer G. Sealy at the International Ornithological Congress in Ottawa, in 1986. (Reproduced courtesy of Spencer G. Sealy).

reviewer trusted by authors and editors looking to vet the quality of their manuscripts. Reviewing hundreds of pages of manuscripts each year, whether at the request of authors, editors, or museum staff, required the investigation of countless fine points of bird biology, distribution, and identification. The 35 000 study specimens that he had acquired during his tenure were no doubt an invaluable resource in mastering these intricate details. It is fair to assume that he personally handled each and every one of these specimens, in addition to the 30 000 or so that were already in the National Museum when he joined it.

It must be remembered that all of these tasks, including the 10 years spent writing the initial edition of *The Birds of Canada*, were over and above his numerous other duties as Curator of Birds, which involved staff supervision, budgeting, and innumerable maintenance issues. One morning in the 1960s, for example, he was shocked to discover that, in his absence, Public Works crews had put the bird cabinets on their sides in order to wash the walls! Major endeavours during his years at the Museum included the creation (starting in 1961) of a brand new Bird Hall in the Victoria Memorial Museum Building and the move of the ornithology collection and research unit out of that building and into the facility at 2379 Holly Lane (in 1972). Anyone familiar with government bureaucracy can easily imagine how much work such undertakings may have necessitated.

Earl's professional activities outside of the Museum walls evolved over time. He frequently gave lectures in the first half of his Ottawa career, but after the publication of his book, when demands on his time became more pressing, his colleagues SDM and Henri Ouellet took over many of the public activities. Earl was Associate Editor of *The Canadian Field-Naturalist* from 1947 to 1976 and from 1990 to 2002, and Associate Editor of *Bird-Banding* from 1948 to 1955. He became Elective Member of the American Ornithologists' Union (A.O.U.) in 1949, Fellow in 1955, and was elected to Council in 1961. He was also on the Program Committee for the A.O.U. annual meetings in the early 1960s, and, in the same period, did brief stints on the A.O.U. Brewster Award Committee and on the Committee on Vernacular Names, as well as on the A.O.U. Committee on Biography in 1969-1972. In 1961, he was appointed to membership in the Cornell University Laboratory of Ornithology, and, in the late 1960s, he joined the National Research Council's Committee on Bird Hazards to Aircrafts. Upon his retirement in 1977 from the (then) National Museum of Natural Sciences, Earl was appointed Curator Emeritus, and became Research Associate

when such a position was reactivated at the Canadian Museum of Nature in 1993. In these capacities, he continued to work (unpaid) on an almost daily basis in his museum office, for 20 years after retirement.

Recognition

Professional recognition came mainly after the publication of *The Birds of Canada*. He received a $1000 Public Service Merit Award in 1965, a substantial amount at the time [although the book was not yet out at that date, the manuscript was important enough to deserve pre-publication recognition]. In 1962, he was elected to serve as Canadian representative to the International Ornithological Congress, and in 1969 he received an honorary Ph.D. from his alma mater, Acadia University. In 1976, Earl was made Corresponding Member of the British Ornithologists' Union, and Honorary Member of the Ottawa Field-Naturalists' Club (which he had first joined in 1930). Recent awards included the first Doris Heustis Speirs Award for contribution to Canadian ornithology (1986), presented to him by the Society of Canadian Ornithologists at the International Ornithological Congress in Ottawa; the first Distinguished Ornithologist Award and Honorary Life Membership in the Ontario Field Ornithologists (1997), for his outstanding contribution to the scientific study of birds in Ontario and Canada; and the Ludlow Griscom Award of the American Birding Association (2000) for publications in field ornithology. Allan Phillips also named a subspecies of the Varied Thrush after him: *Geocichla naevia godfreii*[9].

Earl's commitment to the dissemination of scientific information about birds went far beyond the numerous publications that he authored (see Appendix 2 — his publications in *The Canadian Field-Naturalist* alone span a period of 63 years). The following excerpt from his report of activities for 1970 clearly illustrates his philosophy:

> "For many years, the professional and amateur ornithologists of this country, and the public, have looked to this institution as to no other for information, advice, and services concerning birds and bird study. Several hundred such requests were directed here this year by telephone, personal interview (I personally received 155 visitors to my office), and correspondence, many of which required compilation and/or research. Although extremely time-consuming, I feel strongly that this is a healthy condition and a most important aspect of our work."

Earl Godfrey's legacy to the field of ornithology, especially in Canada, remains profound. The permanent Canada-wide impact of his book published in two languages has set a world-wide standard of ornithological excellence. As a scientist he published nearly a hundred scientific papers, all carefully researched, meticulously accurate, and beautifully written. He also published numerous reviews of the work of others, and contributed thoughtful and perceptive obituaries about colleagues who had preceded him. Naturalists at all levels will always be profoundly grateful to Earl for sharing with them so graphically and enduringly his life-long interest in the birds around us.

Acknowledgments

Anne Marie Barter, Colin Bowen, Dan Brunton, David Campbell, Francis Cook, Charles Douglas, Barbara Erickson, Carol German, Stuart Houston, Virginia Krumholz, Maureen Myers, and Ron Pittaway, among others, have provided material for this article.

End Notes

1. See Godfrey, W. E. 1984. A tribute to Robie Wilfred Tufts, 1884-1982. Canadian Field-Naturalist 98: 513–518.

2. See Aldrich, J. W. 1968. In memoriam: Harry Church Oberholser. Auk 85: 25–29.

3. See Godfrey, W. E. 1988. A tribute to Austin Loomer Rand, 1905-1982. Canadian Field-Naturalist 102: 564–566.

4. See Cranmer-Byng, J. L. 1996. A Life with Birds: Percy A. Taverner, Canadian Ornithologist, 1875-1947. Canadian Field-Naturalist 110: 1–254.

5. See McNeil, R., and W. E. Godfrey. 2000. A tribute to Henri Roger Ouellet, 1938-1999. Canadian Field-Naturalist 114: 154–164.

6. See Ginns, J., and S. Darbyshire. 2001. A tribute to Douglas Barton Osbourne Savile, 1909-2000. Canadian Field-Naturalist 115: 357-364; Godfrey, W. E. 1969. Alfred Eugene Bourguignon 1893-1968. Canadian Field-Naturalist 83: 272-274; and Banim, F. E. 1975. Rowley Campbell Frith, 1897-1974. Canadian Field-Naturalist 89: 470–472.

7. See Cook, F. R. 1986. Editor's Addendum. Canadian Field-Naturalist 100: 279.

8. See Soper, J. H., and E. L. Bousfield. 1982. A tribute to William Willocks Kirwan Baldwin, M. B. E. (1910-1979). Canadian Field-Naturalist 96: 92–97.

9. See Phillips, A. R. 1991. The known birds of North and Middle America, Part II. Allan R. Phillips, Denver.

Accepted 18 March 2003

Other tributes to W. Earl Godfrey

Houston, C. S., and **M. Gosselin.** 2003. In memoriam: W. Earl Godfrey, 1910-2002. Auk 120(1): 196–198.

Mills, E. L. 2002. A tribute to Earl Godfrey. Trail & Landscape 36(4): 135–137.

Mills, E. L. 2002. A tribute to Earl Godfrey. Birders Journal 11(3): 108–109.

Erskine, A. J. 2002. W. Earl Godfrey (1910-2002) — a personal remembrance. Picoides 15(3): 5.

Pittaway, R. 2003. In memoriam: William Earl Godfrey (1910-2002). Ontario Birds 21(1): 43–47.

Appendix 1: Ornithological expeditions by national museum staff under the tenure of W. Earl Godfrey.

Compiled by MICHEL GOSSELIN.

Year	Localities	Investigators
1947	Quebec: Lake Mistassini, Lake Albanel	W. E. Godfrey, W. A. Morris, and R. O. Standfield
1948	Saskatchewan: Cypress Hills, Flotten Lake	W. E. Godfrey, S. D. MacDonald, and R. O. Standfield
1949	Northwest Territories: Mould Bay	S. D. MacDonald
1949	Yukon: Kluane Lake, Carcross	W. E. Godfrey, I. V. F. Allen, and C. L. Thacker
1950	Alberta: Peace River, Grimshaw	W. E. Godfrey, I. V. F. Allen, S. D. MacDonald, and C. D. Waterston
1951	Manitoba: Rennie, Red Deer River	W. E. Godfrey and C. L. Thacker
1951	Nunavut: Ellesmere Island	S. D. MacDonald
1952	Prince Edward Island; Quebec: Gaspé	W. E. Godfrey and J. A. Crosby
1952	British Columbia: Flathead Valley	C. L. Thacker
1952	Northwest Territories: Mould Bay	S. D. MacDonald
1953	British Columbia: Kootenay District	W. E. Godfrey and S. W. Gorham
1954	Nunavut: Isachsen	S. D. MacDonald and G. Blanchard
1954	Nova Scotia: Cape Breton Island	W. E. Godfrey and R. J. D'Entremont
1955	Quebec: Eastern Townships, Gaspé	W. E. Godfrey and R. J. D'Entremont
1955	Nunavut: Eureka	S. D. MacDonald
1956	Manitoba: Windygates; Saskatchewan: Maple Creek; Alberta: Walsh; British Columbia: Elko	W. E. Godfrey and R. J. D'Entremont
1956	British Columbia: Topley, Valemount	S. D. MacDonald
1957	New Brunswick	W. E. Godfrey, R. McNeil, and H. Ouellet
1958	Quebec: Schefferville; Labrabor: Stinson Lake, Sawbill	R. McNeil and H. Ouellet
1958	Northwest Territories: Mackenzie River; Yukon: Herschel Island	S. D. MacDonald and W. J. Smith
1958	Quebec: Gracefield, Camp Dorval; Ontario: Kemptville	D. H. Johnston, G. Blanchard, and S. W. Gorham
1959	Quebec: Sainte-Anne Lake	H. Ouellet and R. Ouellet
1959	Newfoundland: St. Georges, Avalon Peninsula	H. Ouellet
1960	Nunavut: McConnell River	S. D. MacDonald
1960	Labrabor: Coast	H. Ouellet
1961	Quebec: North Shore of St. Lawrence River	H. Ouellet
1962	British Columbia: Dease Lake	S. D. MacDonald, J. Keizer, and I. Stirling
1963	Quebec: Kamouraska County, Anticosti Island	H. Ouellet
1964	British Columbia: Lytton, Williams Lake; Alberta: Banff, Lake Louise, Waterton Lakes	W. E. Godfrey, S. D. MacDonald, J. A. Hanson, and T. A. Willock
1965	Quebec: Abitibi	W. E. Godfrey and E. H. Miller
1966	Ontario: Iron Bridge	W. E. Godfrey and F. Cosenzo
1967	Ontario: Gravenhurst	W. E. Godfrey and F. Cosenzo
1968	Saskatchewan: Fort Carlton	W. E. Godfrey and F. Cosenzo
1969	British Columbia: Prince George	W. E. Godfrey and H. Hiemstra
1971	Quebec: Otish Mountains, Kuujjuarapik	H. Ouellet, J. L. DesGranges, and H. Hiemstra
1972	Quebec: James Bay	H. Ouellet, M. Giroux, and R. M. Poulin
1973	Quebec: Ungava Bay	H. Ouellet, H. Hiemstra, and R. M. Poulin
1974	Quebec: Leaf River	H. Ouellet, R. M. Poulin, and G. Trencia
1975	Quebec: Ford Lake; Nunavut: Coats Island	H. Ouellet, R. M. Poulin, and B. Lyon
1975	Nunavut: Home Bay	B. Knudsen
1976	Nunavut: Home Bay	B. Knudsen
1976	Quebec: North Shore of St. Lawrence River	H. Ouellet and R. M. Poulin

Appendix 2: Publications of [and taxa described by] W. Earl Godfrey.

Compiled by MICHEL GOSSELIN.

Godfrey, W. E. 1938. Yellow-crowned Night Herons in Nova Scotia. Canadian Field-Naturalist 52: 109.

Godfrey, W. E. 1942. Bleak pasture. Explorer / Bulletin of the Cleveland Museum of Natural History 70: 3–4.

Godfrey, W. E. 1942. Census of wintering waterfowl, 1941-1942. [Cleveland] Bird Calendar 38 (3): 2–4.

Godfrey, W. E. 1943. Birds inspect an Ohio museum. Bird-Life [Cleveland Bird Club] 39 (1): 24–28.

Godfrey, W. E. 1943. Hoover Warbler in Ohio. Bird-Life [Cleveland Bird Club] 39 (4): 226.

Godfrey, W. E. 1943. Downtown ornithology. Explorer / Bulletin of the Cleveland Museum of Natural History 74: 6.

Godfrey, W. E. 1943. Audubon's Warbler in Ohio. Auk 60: 451–452.

Godfrey, W. E. 1943. Eared Grebe in Ohio. Auk 60: 452.

Godfrey, W. E. 1944. Five birds unusual in Arizona. Auk 61: 149–150.

Godfrey, W. E. 1945. Sitka Crossbills in Massachusetts. Auk 62: 151.

Godfrey, W. E. 1946. A new Carolina Wren. Auk 63: 564–568. [*Thryothorus ludovicianus alamoensis*]

Godfrey, W. E. 1946. Comment on the record. Cleveland Bird Calendar 42 (1): 7–8.

Godfrey, W. E. 1946. Comments on migration and on the period as a whole. Cleveland Bird Calendar 42 (2): 8.

Godfrey, W. E. 1946. Comment on the record. Cleveland Bird Calendar 42 (4): 9.

Godfrey, W. E. 1946. The American Avocet in Ohio. Cleveland Bird Calendar 42 (4): 13.

Godfrey, W. E. 1947. A new Long-eared Owl. Canadian Field-Naturalist 61: 196–197. [*Asio otus tuftsi*]

Godfrey, W. E. and **A. L. Wilk.** 1948. Birds of the Lake St. John region, Quebec. National Museum of Canada, Bulletin 110.

Godfrey, W. E. 1948. Erroneous use of the name 'Red-backed Junco'. Canadian Field-Naturalist 62: 124.

Godfrey, W. E. 1949. European Starling reaches the Pacific coast. Canadian Field-Naturalist 63: 165.

Godfrey, W. E. 1949. Birds of Lake Mistassini and Lake Albanel, Quebec. National Museum of Canada, Bulletin 114.

Godfrey, W. E. 1949. Distribution of the races of the Swamp Sparrow. Auk 66: 35–38.

Godfrey, W. E. 1950. When the crossbills come. Ottawa Field-Naturalists' Club Newsletter 8: 5.

Godfrey, W. E. 1950. Description of a new northwestern *Geothlypis*. Canadian Field-Naturalist 64: 104. [*Geothlypis trichas yukonicola*]

Godfrey, W. E. 1950. Zoological investigations in western Saskatchewan. National Museum of Canada, Bulletin 118: 93–94.

Godfrey, W. E. 1950. Birds of the Cypress Hills and Flotten Lake Regions, Saskatchewan. National Museum of Canada, Bulletin 120.

Godfrey, W. E. 1950. Notes on the birds of southern Yukon Territory. National Museum of Canada, Bulletin 123: 88–115.

Godfrey, W. E. 1951 Geographical variation in the Boreal Chickadee east of the Rockies. Canadian Field-Naturalist 65: 22–26. [*Parus hudsonicus farleyi*]

Godfrey, W. E. 1951. The Nevada Cowbird at James Bay, Ontario. Canadian Field-Naturalist 65: 46.

Godfrey, W. E. 1951. Comments on the races of the Myrtle Warbler. Canadian Field-Naturalist 65: 166–167.

Godfrey, W. E. 1951. A new northwestern Olive-backed Thrush. Canadian Field-Naturalist 65: 172-174. [*Hylocichla ustulata incana*]

Godfrey, W. E. 1951. Brünnich Murres visit Ottawa. Ottawa Field-Naturalists' Club Newsletter 9: 6–7.

Godfrey, W. E. 1952. Erroneous records of *Empidonax wrightii* in Manitoba and at Belvedere, Alberta. Canadian Field-Naturalist 66: 89.

Godfrey, W. E. 1952. Birds of the Lesser Slave Lake — Peace River areas, Alberta. National Museum of Canada, Bulletin 126: 142–175.

Godfrey, W. E. 1953. Notes on birds of the area of Intergradation between Eastern Prairie and Forest in Canada. National Museum of Canada, Bulletin 128: 189–240.

Godfrey, W. E. 1953. Notes on Ellesmere Island birds. Canadian Field-Naturalist 67: 89–93.

Godfrey, W. E. 1954. The Cattle Egret at sea off Newfoundland. Canadian Field-Naturalist 68: 139–140.

Godfrey, W. E. 1954. Birds of Prince Edward Island. National Museum of Canada, Bulletin 132: 155–213.

Godfrey, W. E. 1954. The Dickcissel on the Atlantic coast of Canada. Auk 71: 317-318.

Godfrey, W. E. 1955. Beaks and feet of birds. Canadian Nature 17: 133-138.

Godfrey, W. E. 1955. Additional notes on birds of the East Kootenay, British Columbia. National Museum of Canada, Bulletin 136: 85–94.

Godfrey, W. E. 1956. Some distributional notes on Canadian birds. Canadian Field-Naturalist 70: 136–137.

Godfrey, W. E. 1956. The Little Egret, a new bird for North America. Auk 73: 457.

Godfrey, W. E. 1956. Some Canadian Birds. National Museum of Canada, Ottawa.

Godfrey, W. E. 1957. Quelques oiseaux du Canada. Musée national du Canada, Ottawa.

Godfrey, W. E. 1957. Warblers in the Prairie Provinces. Chapter 18 *in* The Warblers of America. *Edited by* L. Griscom and A. Sprunt Jr. Devin-Adair, New York.

Godfrey, W. E. 1958. Birds. Pages 396–397 *in* Encyclopedia Canadiana. Canadiana Co. Ltd, Ottawa.

Godfrey, W. E. 1958. Birds of Cape Breton Island, Nova Scotia. Canadian Field-Naturalist 72: 7–27.

Godfrey, W. E. 1958. Christmas bird census — 1957. Canadian Field-Naturalist 72: 32–47.

Godfrey, W. E. 1959. Christmas bird census — 1958. Canadian Field-Naturalist 73: 29–47.

Godfrey, W. E. 1959. Notes on the Great Auk in Nova Scotia. Canadian Field-Naturalist 73: 175.

Godfrey, W. E. 1959. The Common Scoter on Cape Breton Island, Nova Scotia — a correction. Canadian Field-Naturalist 73: 184.

Godfrey, W. E. 1959. Ornithological investigations in the Schefferville area. McGill Sub-Arctic Research Papers 6: 32–33.

Godfrey, W. E. 1960. Christmas bird census — 1959. Canadian Field-Naturalist 74: 28–49.

Godfrey, W. E. 1961. Notes on Newfoundland birds. National Museum of Canada, Bulletin 172: 98–111.

Godfrey, W. E. 1961. First Canadian record of the Black-throated Sparrow. Canadian Field-Naturalist 75: 162.

Godfrey, W. E. 1962. A Saskatchewan specimen of the Greater Scaup. Canadian Field-Naturalist 76: 125.

Godfrey, W. E. 1962. Common Loon. Yellow-billed Loon. Arctic Loon. Red-throated Loon. Pages 21–25, 33–38, 40–44, 48-53, 59-61 *in* Handbook of North American Birds. Volume 1. *Edited by* R. S. Palmer. Yale University Press, New Haven.

Godfrey, W. E. 1965. The gender of the fringillid genus *Pinicola*. Auk 82: 273.

Godfrey, W. E. 1965. Range extensions of some birds in western Mackenzie. Canadian Field-Naturalist 79: 34–38.

Godfrey, W. E. 1965. An erroneous record of the Gray-cheeked Thrush in Saskatchewan. Canadian Field-Naturalist 79: 155–156.

Godfrey, W. E. 1966. Some Canadian birds. Revised Edition. National Museum of Canada, Ottawa.

Godfrey, W. E. 1966. The supposed nesting of the Slaty-backed Gull in Canada. Canadian Field-Naturalist 80: 48–49.

Godfrey, W. E. 1966. A Summer Tanager in Manitoba. Canadian Field-Naturalist 80: 254.

Godfrey, W. E. 1966. Clay-colored Sparrow nesting at Ottawa, Ontario. Canadian Field-Naturalist 80: 255–256.

Godfrey, W. E. 1966. The Birds of Canada. National Museum of Canada, Bulletin 203.

Godfrey, W. E. 1967. Les oiseaux du Canada. Musée national du Canada, Bulletin 203.

Godfrey, W. E. 1967. Some winter aspects of the Great Gray Owl. Canadian Field-Naturalist 81: 99–101.

Godfrey, W. E. 1967. Xanthochroism in the Cape May Warbler and Evening Grosbeak. Canadian Field-Naturalist 81: 226–227.

Godfrey, W. E. 1968. The birds of Canada. Pages 50–51 *in* Canada Year Book 1968. Dominion Bureau of Statistics, Ottawa.

Godfrey, W. E. 1968. Les oiseaux du Canada. Pages 55–56 *in* Annuaire du Canada 1968. Bureau fédéral de la Statistique, Ottawa.

Godfrey, W. E. 1968. The Evening Grosbeak. Trail & Landscape 2: 4-6.

Godfrey, W. E. 1968. Notes on birds of the Amos region, Quebec. National Museum of Canada, Natural History Papers 44.

Godfrey, W. E. 1969. Notes on birds of the Iron Bridge, Ontario, Region. Canadian Field-Naturalist 83: 158–159.

Godfrey, W. E. 1969. Alfred Eugene Bourguignon 1893-1968. Canadian Field-Naturalist 83: 272–274.

Godfrey, W. E. 1969. The Golden-winged Warbler in Muskoka County, Ontario. Canadian Field-Naturalist 83: 281.

Godfrey, W. E. 1969. Nesting of the Caspian Tern in central-eastern Manitoba. Canadian Field-Naturalist 83: 401.

Godfrey, W. E. 1969. The breeding status of the Black-necked Stilt in Canada. Auk 86: 562–563.

Godfrey, W. E. 1970. Canada's endangered birds. Canadian Field-Naturalist 84: 24–26.

Godfrey, W. E. 1970. Endangered wildlife - birds. Pages 8-9 *in* Endangered Wildlife in Canada. Canadian Wildlife Federation, Ottawa.

Godfrey, W. E. 1971. In memoriam: Albert Ellis Allin. Auk 88: 225–226.

Godfrey, W. E. 1972. In memoriam: Lewis McIver Terrill. Canadian Field-Naturalist 86: 87–90.

Godfrey, W. E. 1972. Encyclopédie des oiseaux du Québec. Éditions de l'Homme, Montréal.

Godfrey, W. E. 1972. North American Ruddy Turnstones in Britain. Bulletin of the British Ornithologists' Club 92: 148.

Godfrey, W. E. 1973. A possible shortcut spring migration route of the Arctic Tern to James Bay, Canada. Canadian Field-Naturalist 87: 51–52.

Godfrey, W. E. 1973. More presumed hybrid gulls: *Larus argentatus* x *L. marinus*. Canadian Field-Naturalist 87: 171-172.

Godfrey, W. E. 1973. Recent changes in bird names. Canadian Field-Naturalist 87: 473.

Godfrey, W. E. 1974. Sight records of birds. Canadian Field-Naturalist 88: 107.

Godfrey, W. E. 1974. Introduction. Page 1 *in* Taverner's Birds of Eastern Canada. *By* P. A. Taverner. Reprinted Coles Publishing, Toronto.

Godfrey, W. E. 1975. Birds. Page 396–397 *in* Encyclopedia Canadiana. Grolier of Canada, Toronto.

Godfrey, W. E. 1975. More dwarf passerine eggs. Canadian Field-Naturalist 89: 189.

Godfrey, W. E. 1975. The Cardinal nesting in Ottawa. Trail & Landscape 9: 10–11.

Godfrey, W. E. 1976. Breeding status of the Common Redpoll in Alberta and Saskatchewan. Canadian Field-Naturalist 90: 199–200.

Godfrey, W. E. 1976. Audubon's Shearwater, a species new for Canada. Canadian Field-Naturalist 90: 494.

Ouellet, H., and **W. E. Godfrey.** 1980. Ornithology in Canada in the 20th century: a capsule overview. Bulletin of the British Ornithologists' Club 100: 115–118.

Austin, G. T., E. R. Blake, P. Brodkorb, M. R. Browning, W. E. Godfrey, J. P. Hubbard, G. McCaskie, J. T. Marshall Jr., G. Monson, S. L. Olson, H. Ouellet, R. S. Palmer, A. R. Phillips, W. M. Pulich, M. A. Ramos, A. M. Rea, and **D. A. Zimmerman.** 1981. Ornithology as science. Auk 98: 636–637.

Traylor, M. A., D. Amadon, and **W. E. Godfrey.** 1984. In memoriam: Austin L. Rand. Auk 101: 600–602.

Godfrey, W. E. 1984. A tribute to Robie Wilfred Tufts, 1884-1982. Canadian Field-Naturalist 98: 513-518.

Godfrey, W. E. 1985. Bird watching. Page 185 *in* The Canadian Encyclopedia. Hurtig Publishers, Edmonton.

Godfrey, W. E. 1986. The Birds of Canada. Revised Edition. National Museum of Natural Sciences, Ottawa.

Godfrey, W. E. 1986. Les oiseaux du Canada. Édition révisée. Musée national des sciences naturelles, Ottawa.

Godfrey, W. E. 1987. Oiseaux, observation des. Page 1379 *in* L'Encyclopédie du Canada. Alain Stanké, Montréal.

Godfrey, W. E. 1988. A tribute to Austin Loomer Rand, 1905-1982. Canadian Field-Naturalist 102: 564–566.

Cook, F. R., and **W. E. Godfrey.** 1988. A Canadian bibliography of Austin L. Rand. Canadian Field-Naturalist 102: 567–569.

Godfrey, W. E. 1989. Foreword. Pages 9-10 *in* Birds of the Kingston Region. *Edited by* R. D. Weir. Kingston Field Naturalists.

Godfrey, W. E. 1990. Foreword. Page xi *in* The Birds of British Columbia. Volume 1. *Edited by* R. W. Campbell, N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, and M. C. E. McNall. Royal British Columbia Museum.

Godfrey, W. E. 1990. Encyclopédie des oiseaux du Québec. Édition révisée. Éditions de l'Homme, Montréal.

Godfrey, W. E. 1992. Subspecies of the Red Knot *Calidris canutus* in the extreme north-western Canadian arctic islands. Wader Study Group Bulletin 64, Supplement: 24–25.

McNeil, R., and **W. E. Godfrey.** 1999. In memoriam: Henri Roger Ouellet, 1938-1999. Auk 116: 1118–1121.

McNeil, R., and **W. E. Godfrey.** 2000. A tribute to Henri Roger Ouellet, 1938-1999. Canadian Field-Naturalist 114: 154–164.

Godfrey, W. E. 2000. A tribute to John Launcelot Cranmer-Byng, 1919-1999. Canadian Field-Naturalist 114: 710–711.

Houston, C. S., and **W. E. Godfrey.** 2002. In memoriam: Arthur C. Twomey, 1908-1996. Auk 119: 811–812.

Reviews by W. E. Godfrey:

1948. Book reviews: *Silent Wings*. Canadian Field-Naturalist 62: 45.

1948. Book reviews: *Annual Report of the Province of Quebec Society for the Protection of Birds, Inc., for 1946.* Canadian Field-Naturalist 62: 77.

1948. Book reviews: *The Summer Birds of Sudbury District, Ontario*. Canadian Field-Naturalist 62: 101-102.

1948. Book reviews: *Flashing Wings.* Canadian Field-Naturalist 62: 102.

1948. Recent Literature: *A Study of the Winter Feeding Habits of the Short-eared Owl* (Asio flammeus) *in the Toronto Region.* Bird-Banding 19: 127.

1948. Recent Literature: *Clutch Size in the Spruce Grouse and Theoretical Consideration of Some Factors Affecting Clutch Size.* Bird-Banding 19: 128-129.

1949. Recent Literature: *Tradition in Bird Life*. Bird-Banding 20: 61.

1949. Recent Literature: *A Review of the Bird Fauna of British Columbia.* Bird-Banding 20: 72.

1949. Book reviews: *Island Life: A Study of the Land Vertebrates of the Islands of Eastern Lake Michigan.* Canadian Field-Naturalist 63: 45.

1949. Book reviews: *A Review of the Bird Fauna of British Columbia.* Canadian Field-Naturalist 63: 45–46.

1949. Book reviews: *Geographic Variation in Newfoundland Birds.* Canadian Field-Naturalist 63: 92.

1949. Book reviews: *The Ten-Year Cycle*. Canadian Field-Naturalist 63: 118.

1949. Reviews: *Fluctuations in Animal Populations with Special Reference to Those of Canada.* Canadian Field-Naturalist 63: 118.

1949. Book reviews: *Know Your Ducks and Geese.* Canadian Field-Naturalist 63: 241.

1950. Review: *The Second Annual Report of the Wildfowl Trust, The New Grounds, Slimbridge, Gloucestershire, England.* Canadian Field-Naturalist 64: 126.

1950. Reviews: *The Sandhill Cranes.* Canadian Field-Naturalist 64: 156.

1950. Reviews: *Bird-Watching.* Canadian Field-Naturalist 64: 157–158.

1950. Reviews: *Audubon's Birds of America.* Canadian Field-Naturalist 64: 190.

1950. Reviews: *National Wildlife and Conservation Digest, Vol. 1, No. 1, January, 1950, pp. 1-112.* Canadian Field-Naturalist 64: 190.

1950. Reviews: *Annual Report for 1948 of the Province of Quebec Society for the Protection of Birds, Inc., Montreal, P.Q., pp. 1-41.* Canadian Field-Naturalist 64: 220.

1950. Reviews: *W. E. Saunders, Naturalist.* Canadian Field-Naturalist 64: 220.

1950. Reviews: *An Annotated List of the Birds of the East Kootenay, British Columbia.* Canadian Field-Naturalist 64: 220.

1950. Recent Literature: *The Red Crossbill at Pimisi Bay, Ontario.* Bird-Banding 21: 26.

1950. Recent Literature: *The Wild Turkey in Ontario.* Bird-Banding 21: 33.

1950. Recent Literature: *Nesting of the Red Crossbill in Pakenham Township, Lanark County, Ontario.* Bird-Banding 21: 158.

1950. Recent Literature: *Birds of the Lake St. John Region, Quebec.* Bird-Banding 21: 165.

1950. Recent Literature: *Birds of Southern Alberta.* Bird-Banding 21: 172.

1951. Recent Literature: *Some Counts of Bird Populations in Coniferous Forests near the Limit of Trees.* Bird-Banding 22: 189.

1951. Reviews: *A New Subspecies of Moose from North America.* Canadian Field-Naturalist 65: 84.

1951. Reviews: *A Study of Bird Populations in the Apple Orchards of the Annapolis Valley, Nova Scotia, with Particular Reference to the Effects of Orchard Sprays Upon Them.* Canadian Field-Naturalist 65: 84.

1951. Reviews: *Prince Albert National Park Creel Census Analysis, Season 1948.* Canadian Field-Naturalist 65: 84.

1951. Reviews: *Canada Geese of the Mississippi Flyway with Special Reference to an Illinois Flock.* Canadian Field-Naturalist 65: 84–85.

1951. Reviews: *The Mammals of Watertown Lakes National Park.* Canadian Field-Naturalist 65: 85.

1951. Reviews: *The Birds and Mammals of the Creston Region, British Columbia.* Canadian Field-Naturalist 65: 85–86.

1951. Reviews: *Studies in Bird Migration Being the Collected Papers of H. Chr. C. Mortensen, 1856-1921.* Canadian Field-Naturalist 65: 86.

1951. Book Reviews: *The Birds of Greenland.* Canadian Field-Naturalist 65: 124.

1951. Reviews: *Dawn Song and All Day.* Canadian Field-Naturalist 65: 188–189.

1951. Reviews: *Migration of Birds*. Canadian Field-Naturalist 65: 189.

1951. Reviews: *Nature through the Year.* Canadian Field-Naturalist 65: 190.

1952. Reviews: *The Birds of Newfoundland.* Canadian Field-Naturalist 66: 69-70.

1952. Reviews: *Bird Guide. Land Birds East of the Rockies.* Canadian Field-Naturalist 66: 70.

1952. Reviews: *Carolina Quest.* Canadian Field-Naturalist 66: 90.

1952. Reviews: *A Guide to Bird Finding East of the Mississippi.* Canadian Field-Naturalist 66: 92–93.
1952. Book Reviews: *The Birds of Greenland.* Canadian Field-Naturalist 66: 114.
1952. Book Reviews: *Arizona and its Bird Life.* Canadian Field-Naturalist 66: 117.
1952. Book Reviews: *Stalking Birds with Color Camera.* Canadian Field-Naturalist 66: 118.
1952. Reviews: *The Birds of Greenland.* Canadian Field-Naturalist 66: 147.
1952. Reviews: *Check-list of North American Birds and Synopsis of the North American Mammals.* Canadian Field-Naturalist 66: 148.
1952. Reviews: *Variation in* Anas cyanoptera. Canadian Field-Naturalist 66: 175.
1952. Reviews: *A Pocket-Book of Lesser-Known British Birds.* Canadian Field-Naturalist 66: 176.
1952. Recent Literature: *The Birds of Newfoundland.* Bird-Banding 23: 46–47.
1952. Recent Literature: *A Study of Screech Owls in Southern Ontario.* Bird-Banding 23: 172.
1952. Recent Literature: *The Upland Sandpiper in Southwestern Yukon Territory.* Bird-Banding 23: 178.
1952. Recent Literature: *Study of Bird Populations in the Apple Orchards of the Annapolis Valley, Nova Scotia, with Particular Reference to the Effects of Orchard Sprays Upon Them.* Bird-Banding 23: 180.
1952. Recent Literature: *Observations of Ruffed Grouse in Southern Ontario with a Discussion of Cycles.* Bird-Banding 23: 180–181.
1952. Recent Literature: *Breeding Behaviour of the Ring-necked Pheasant on Pelee Island, Ontario.* Bird-Banding 23: 181.
1952. Recent Literature: *Colour Phase Investigations on the Screech Owl in Ontario.* Bird-Banding 23: 186.
1952. Recent Literature: *Check-list of North American Birds and Synopsis of the North American Mammals.* Bird-Banding 23: 193.
1953. Recent Literature: *The Birds of Elk Island National Park, Alberta, Canada.* Bird-Banding 24: 30.
1953. Recent Literature: *The Birds of Prince Albert National Park, Saskatchewan.* Bird-Banding 24: 30.
1953. Recent Literature: *The Economic Status of the Herring Gulls of the Grand Manan Archipelago, New Brunswick, 1949.* Bird-Banding 24: 113.
1953. Recent Literature: *The Birds of New Brunswick.* Bird-Banding 24: 124.
1954. Reviews: *The Birds of New Brunswick.* Canadian Field-Naturalist 68: 45–46.
1954. Reviews: *The Eastern Belted Kingfisher in the Maritime Provinces.* Canadian Field-Naturalist 68: 46.
1954. Recent Literature: *On Eastern Empidonaces with Particular Reference to Variation in* E. traillii. Bird-Banding 25: 30.
1954. Recent Literature: *Birds of the West James Bay and Southern Hudson Bay Coasts.* Bird-Banding 25: 31.
1954. Recent Literature: *The Eastern Belted Kingfisher in the Maritime Provinces.* Bird-Banding 25: 80.
1954. Recent Literature: *Chimney Swift Banding at Kingston, Ontario, from 1928 to 1947.* Bird-Banding 25: 115.
1954. Recent Literature: *A Brief Study of the Double-crested Cormorant on Lake Winnipegosis.* Bird-Banding 25: 128.
1955. Recent Literature: *Summer Birds of Western Ontario.* Bird-Banding 26: 38–39.
1955. Amongst the new books: *Eagles.* Canadian Geographical Journal 51 (6): xi.
1955. Reviews: *Audubon Guides. All the Birds of Eastern and Central North America.* Canadian Field-Naturalist 69: 28.
1955. Reviews: *The Lives of Wild Birds.* Canadian Field-Naturalist 69: 30.
1955. Reviews: *Summer Birds of Western Ontario.* Canadian Field-Naturalist 69: 68–69.
1955. Reviews: *An Introduction to Ornithology.* Canadian Field-Naturalist 69: 134.
1956. Reviews: *The Geography, Birds, and Mammals of the Perry River Region.* Canadian Field-Naturalist 70: 147–148.
1957. Reviews: *The Birds of Massachusetts.* Canadian Field-Naturalist 71: 84–85.
1957. Reviews: *Audubon Western Bird Guide.* Canadian Field-Naturalist 71: 200–201.
1957. Reviews: *A Laboratory and Field Manual of Ornithology.* Canadian Field-Naturalist 71: 206–207.
1958. Reviews: *The Breeding Biology of the Chimney Swift* Chaetura pelagica *(Linnaeus).* Canadian Field-Naturalist 72: 176.
1958. Reviews: *Warblers—Songs of Warblers of Eastern North America.* Canadian Field-Naturalist 72: 176.
1958. Reviews: *The Behavioral, Ecological and Morphological Characteristics of Two Populations of the Alder Flycatcher,* Empidonax traillii *(Audubon).* Canadian Field-Naturalist 72: 182.
1959. Amongst the new books: *The Birds of the Saskatchewan River, Carlton to Cumberland.* Canadian Geographical Journal 60 (1): v-vi.
1959. Blue Jay Bookshelf: *The Birds of the Saskatchewan River, Carlton to Cumberland.* Blue Jay 17: 171–172.
1959. Reviews: *Changes in the Fauna of Ontario.* Canadian Field-Naturalist 73: 132.
1959. Reviews: *The Birds of Alaska.* Canadian Field-Naturalist 73: 180–181.
1960. Reviews: *Feathers and Flight.* Canadian Field-Naturalist 74: 57–58.
1960. Reviews: *The Birds of the Saskatchewan River, Carlton to Cumberland.* Canadian Field-Naturalist 74: 166.
1960. Reviews: *A Field List of Birds of the Detroit-Windsor Region.* Canadian Field-Naturalist 74: 182.
1960. Reviews: *Finches: Songs of Fringillidae of Eastern and Central North America.* Canadian Field-Naturalist 74: 184.
1961. Reviews: *A Gathering of Shore Birds.* Canadian Field-Naturalist 75: 103.
1961. Reviews: *Birds of Regina.* Canadian Field-Naturalist 75: 261.
1962. Reviews: *Birds of the Caribbean.* Canadian Field-Naturalist 76: 116.
1963. Reviews: *The Birds of Nova Scotia.* Canadian Field-Naturalist 77: 124–125.
1964. Reviews: *The Birds.* Canadian Field-Naturalist 78: 56–57.
1964. Reviews: *Birds of the Labrador Peninsula and Adjacent Areas.* Canadian Field-Naturalist 78: 119–120.

1964. Reviews: *Birds of the Lake Athabaska Region.* Canadian Field-Naturalist 78: 120.
1964. Reviews: *Where is That Vanished Bird?* Canadian Field-Naturalist 78: 193–194.
1965. Reviews: *Geographic Variation in the White-crowned Sparrow* Zonotrichia leucophrys. Auk 82: 510–511.
1965. Reviews: *Birds over America.* Canadian Field-Naturalist 79: 72.
1965. Reviews: *Biosystematics of Sibling Species of Flycatchers in the* Empidonax hammondii — oberholseri — wrightii *Complex.* Canadian Field-Naturalist 79: 72.
1965. Reviews: *The World of Birds.* Canadian Field-Naturalist 79: 145.
1965. Reviews: *Life Histories of North American Birds.* Canadian Field-Naturalist 79: 145–146.
1965. Reviews: *Studies in the Life History of the Song Sparrow.* Canadian Field-Naturalist 79: 146.
1965. Reviews: *The Story of My Pelican.* Canadian Field-Naturalist 79: 146.
1965. Reviews: *Three Bird Immigrants from the Old World.* Canadian Field-Naturalist 79: 146–147.
1966. Reviews: *Birds of Prey of the World.* Canadian Field-Naturalist 80: 57.
1966. Reviews: *A New Dictionary of Birds.* Canadian Field-Naturalist 80: 111.
1967. Reviews: *History of the Birds of Kingston, Ontario.* Canadian Field-Naturalist 81: 75.
1967. Reviews: *The Whooping Crane.* Canadian Field-Naturalist 81: 144–145.
1967. Reviews: *John James Audubon, A Biography.* Canadian Field-Naturalist 81: 145–146.
1967. Reviews: *A Guide to Field Identification, Birds of North America.* Canadian Field-Naturalist 81: 146.
1967. Reviews: *North American Birds Eggs.* Canadian Field-Naturalist 81: 213-214.
1967. Reviews: *Living Island.* Canadian Field-Naturalist 81: 217.
1968. Reviews: *The Shell Bird Book.* Canadian Field-Naturalist 82: 59.
1968. Reviews: *A Comparative Life-history Study of Four Species of Woodpeckers.* Canadian Field-Naturalist 82: 160.
1968. Reviews: *The Shorebirds of North America.* Canadian Field-Naturalist 82: 232.
1968. Reviews: *Birds in Our Lives.* Canadian Field-Naturalist 82: 232–233.
1968. Reviews: *The Birds of Simcoe County, Ontario.* Canadian Field-Naturalist 82: 302.
1969. Reviews: *Hours and the Birds.* Canadian Field-Naturalist 83: 69–70.
1969. Reviews: *A Lifetime with the Birds: An Ornithological Logbook.* Canadian Field-Naturalist 83: 70.
1970. Reviews: *Eagles, Hawks and Falcons of the World.* Canadian Field-Naturalist 84: 323.
1971. Reviews: *Birds of the Churchill Region, Manitoba.* Canadian Field-Naturalist 85: 272.
1972. Reviews: *Pictorial Guide to the Birds of North America.* Canadian Field-Naturalist 86: 109-110.
1972. Reviews: *Birds of Guatemala.* Canadian Field-Naturalist 86: 201–202.
1973. Book Reviews: *Birds of Moose Mountain, Saskatchewan.* Canadian Field-Naturalist 87: 199.
1974. Book Reviews: *Grzimek's Animal Life Encyclopedia.* Canadian Field-Naturalist 88: 521.
1974. Ornithological Literature: *Alberta Vireos and Wood Warblers.* Wilson Bulletin 86: 189–190.
1975. Book Reviews: *Wildlife in North America: Birds.* Canadian Geographical Journal 91 (4): 43.

Book Reviews

ZOOLOGY

Sibley's Birding Basics

By David A Sibley. 2002. Alfred A. Knopf, New York. 154 pp., illus. U.S. $15.95.

My copy of this book arrived four days before I was to give a six-session course in birding basics to a group of children. The book was immediately useful as a review document. Had I left anything important out of the curriculum? Were there better ways of getting the message across? I was relieved to find that Sibley and I had similar ideas on the fundamentals. I was delighted to use some of his ideas to improve my course. There was one key difference. Sibley's focus is on bird identification, whereas I planned to introduce the children to some biology too.

This is a small, 5" (13 cm) × 8" (21 cm), pocket book that discusses all the techniques used in bird identification. It goes beyond the classic use of field marks and shows the value of peripheral clues such as habitat, weather, and behaviour. The author discusses detail on feather patterns and arrangements, as well as moult and wear. Bare parts and voice are also covered.

This book has more coverage on feathers and feather groups than any other text I have seen. I think this is very helpful to beginners. Sibley starts with the typical passerine diagram of feather distribution and illustrates a further nine species with a total of 14 drawings. For example, it allows the novice to see where scapulars occur on birds that are as different as a goose and a hummingbird. The author covers the different types of feathers and their functions. He covers the various moult processes and their effect. Sibley has also included some illustrations of birds in the scrunched and stretched positions to show how these changes affect appearance. He has also shown moult sequences for both the whole bird and wings alone.

The illustrations, both black-and-white and colour, are delightful. Sibley combines his great technical skill with a sound and detailed knowledge of birds. So while the artwork is accurate it is also artistically attractive. In particular, Sibley is able to paint birds at differing angles and stances so that he can illustrate a particular attribute.

There are a couple of places where I have a viewpoint different from the author's. Most beginners find bird songs very difficult to learn. I advise them to learn just one song of a common local bird (e.g., Song Sparrow) until they can identify it with confidence. Then, and only then, choose a second bird. This method avoids that dreadful confusion that beginners experience when they start mixing up songs. The author's advice is quite good, but it is far more valid once people have learned 50 or more songs. I would also have spent more time on the physics of flight, because I think this helps understand the bird's motion. This in turn helps with identification. On the other hand, I thought his section on taxonomy was just right. These types of comments reflect personal choice more than criticism. There were a couple of places where my criticism is more factual. For example, he states that a Hairy Woodpecker is always bigger than a Downy. At the extreme this is not always true.

Although written as a basic text, this book has much to offer all levels of birders. Even the most expert birder will find material to help answer questions posed by novices. I particularly like Sibley's approach and clear explanations for all the aspects of a bird's feathers. This is my first Sibley book, but it will not be my last.

ROY JOHN

2193 Emard Crescent, Ottawa, Ontario K1J 6K5 Canada

Fishes of Alaska

By Catherine W. Mecklenburg, T. Anthony Mecklenburg, and Lyman K. Thorsteinson. 2002. American Fisheries Society, Bethesda, Maryland. xxxvii + 1037 pp., illus. U.S. $129 ($90 for AFS Members).

This tome is the long-awaited definitive book on the Alaskan fishes, an initiative first approved by the Alaska Chapter of the American Fisheries Society in 1989. It is of particular interest to Canadians as it covers the marine ichthyofauna that abuts the Arctic Canadian waters of the Beaufort Sea and, in the south, Canada's Pacific coast of British Columbia. Freshwater fishes are also covered but obligate species number only about 13 out of the 601 species in 108 families treated — all the other species are marine, or at least enter brackish waters or migrate between marine and fresh waters.

The book includes a foreword and preface that outline problems in production, sources used, and methods adopted for accepting records. A short introduction covers history of research, composition of the fauna, endemics, introduced species, habitats, fisheries, geology, the fresh and marine environments, and zoogeography. It is followed by a list of species, an explanation of the layout of species accounts, and a key to families. There are 40 colour plates, each with eight photographs of fish, some in their natural habitat but most laid out in a formal pose. The bulk of the text (800 pages) is the species accounts. These are followed by a gazetteer, a glossary, a bibliography, and an index of scientific and common names.

The individual species accounts are preceded by a family account which can be quite extensive, discussing characters of species, systematic problems, and dubious records. Each species account fills one page and consists of scientific and common name, a brief summary of distribution, a small (71 × 41 mm) standard map with spots or shading (and claiming part of the Beaufort Sea that is Canadian), habitats, meristic characters, bulleted characters ranging from colour to size and various anatomical features, one to several full-page line illustrations of the fish, often with details of key characters, and a notes and sources section that gives synonyms, literature sources for the description, figure sources, and notes on the range of the species. There is no detailed account of such factors as reproduction, age and growth, food, parasites, and other biological data.

The identification keys are positioned in the text before the species accounts. Positioning keys is always a problem as the alternative of grouping all keys together removes them from the species illustrations and relevant text. Either arrangement requires a lot of page turning. While some families have only a single species, or few distinctive species, others have numerous species and the keys are most useful in this regard.

There are 39 species of Scorpaenidae, 35 in one genus, while Cottidae has 87 species (and the family introduction reviews the genera pointing out some unique characters — perhaps a separate generic key would have been easier as 12 pages of alternatives can easily lead one astray).

This is not a field guide. It weighs in at 3.3 kg and is 6 cm thick. In this respect a CD-ROM version would have been a convenient means of carrying the information contained in this book to the field and on other travels.

Any such extensive endeavour can be expected to raise certain questions and contain some errors. Each species account is grouped with species from the same genus and then in the order in which they key out. This is confusing when searching for a species account, e.g. in *Sebastes*, *aleutianus* is near the end while *nigrocinctus* is the second account. The colour photograph of the Longnose Lancetfish on plate IX shows this fish being held up against a background of a small stream, a rather disconcerting juxtaposition of habitat and fish for an oceanic species (presumably the beach where it washed up is behind the photographer). The glossary defines otolith as "bones of the inner ear" when they are calcium carbonate structures. *Chiasmodon niger* has a publication date of 1863 while Eschmeyer (1998) gives 1864. Coad et al. (1995) is cited in various places in the text but is not in the Bibliography. Although most species are illustrated a few are not, e.g., *Liparis bristolensis*, and a very few are of poor quality; e.g., *Liparis megacephalus*.

The cost is rather high (over $200 Canadian) but the publisher probably needs to recoup some of the costs of production while recognising that this is a technical publication, not a popular guide, and therefore not likely to be bought by those casually interested in Alaskan fishes. We may be reaching the financial limit for production and sale of books of this size and technical scope. I expect that these kinds of works will increasingly appear only on web sites although there are financing and long-term archival and maintenance problems to be solved in this format. The *Catalog of Fishes* appeared as a three-volume book, a CD-ROM, and is also online, the latter method allowing constant updates and corrections, and is a method to follow (Eschmeyer 1998). The authors of *Fishes of Alaska* have researched distributional records and species identities extensively; e.g., on page 403 they cite information dated 5 April 2001 from the Canadian Museum of Nature for *Artediellus uncinatus* limiting it to Davis Strait in the Arctic, but we now have records from Dolphin and Union Strait and the Beaufort Sea and so it may well occur in Alaska — an example of how rapidly our knowledge changes.

The strength of this work lies in its meticulous analysis of distributional records, placing the ichthyofauna of Alaska on a firm footing, and the identification keys coupled with excellent line drawings that enable these fishes to be identified. It will long remain the primary source for information on Alaskan fishes and an essential work for anyone studying fishes from the westernmost Canadian waters of British Columbia and the Arctic.

Literature Cited

Coad, B. W., with **H. Waszczuk** and **I. Labignan**. 1995. Encyclopedia of Canadian Fishes. Museum of Nature, Ottawa, and Canadian Sportfishing Productions, Waterdown, Ontario. viii + 928 pages.

Eschmeyer, W. N. *Editor*. 1998. Catalog of Fishes. California Academy of Sciences, San Francisco. 3 volumes, CD-ROM. www.calacademy.org/research/ichthyology/catalog/fishcatsearch.html.

BRIAN W. COAD

Canadian Museum of Nature, P. O. Box 3443, Station D, Ottawa, Ontario K1P 6P4 Canada

Evolution, Ecology, Conservation, and Management of Hawaiian Birds: A Vanishing Avifauna

Edited by J. M. Scott, S. Conant and C. Van Riper III. 2002. The Cooper Ornithological Society. Distributed by Western Foundation of Vertebrate Zoology, c/o Jon C. Fisher, 439 Calle San Pablo, Camarillo, California 93012-8506 U.S.; (805) 388-9944; wfvz@wfvz.org. 428 pp., illus. Cloth U.S. $48.50; paper U.S. $29.00.

Evolution, Ecology, Conservation and, Management of Hawaiian Birds: A Vanishing Avifauna is a special publication of the Cooper Ornithological Society. It brings together a number of closely related but independent research reports, because, as a group, these reports are too large for the society's regular publication, *The Condor*.

The format of the individual papers is the same as any refereed scientific publication, such as the *Canadian Field-Naturalist*. The editors have arranged the papers into six groups. These are Historical Perspectives, Systematics, Status and Trends, Ecology, Limiting Factors, and Recovery and Management. Each section is preceded by a short introduction and there is a (somewhat larger) general introduction at the beginning of the report as a whole. The literature cited has been combined into a single tabulation at the back of the book.

In the 34 papers the authors give a number of generic overviews and cover 12 species in detail. In particular they look at the effects of introduced pests, including pigs (brought by the original settlers) and rats and goats (released by Europeans), insects, diseases, and plants. Starting from an oceanic paradise, Hawaii has suffered multiple abuses that now manifest themselves as major environmental problems. There are many lessons to be learned here.

With such a diversity of papers it is best to review a selected few and develop a sense of the overall content. The paper by Cornutt and Pimm tackles the difficult problem of developing a list of species for the Central Pacific. A particular challenge is deciding on those species that existed before the arrival of Europeans. This is a complex task of searching archeological, historical and current records. It involves deciding on the existence of species and subspecies, especially island endemics, often with scant evidence.

For the Hawaiian Rare Bird Search, Reynolds and Snetsinger not only used recent historical data but also spent three quarters of their time in the field looking for critical species. Woodworth et al. looked at the breeding productivity and survival of a single species, the Hawaiian Honeycreeper. Their research showed this bird has a low productivity rate with a 70% nesting failure.

Krushelnycky et al. investigated the interaction between the Hawaiian Dark-rumped Petrel and the introduced Argentinean ant. They found that this insect did not appear to have any impact on the bird's success. As ants have a profound influence on the local ecology, the question still remains as to their effect on other native species. Drigot reports on one of the projects to repair past damage. This was done at a military base and the management program successfully combined the requirements of military manœuvers and environmental needs of the subject species, Hawaiian Stilts. Such good news stories need to be well publicized.

There are a number of illustrations. I think these are black-and-white versions of full-colour paintings. The frontispiece is a full-colour picture of an 'O'o.

The authors present the results of good solid scientific work. The information is manipulated and distillated through discussion into ideas and new concepts. The results will be of value to scientists, but some of the papers will be difficult for the non-expert to digest. The publication marks a major milestone in understanding the problems in Hawaii and offers some hope for the future. It is clear though these research projects were opportunistic and took advantage of circumstances (to get funding?) rather than formed part of an integrated plan. The same is true for conservation and restoration projects. These mainly follow either a species or a habitat preservation approach. For true success, all the known limiting factors have to be included: habitat, disease, aliens, competition, predation, disturbance, etc. These papers underscore this statement.

After going through these reports I saw there were some important messages overtly and covertly to be found in the text. These are messages that must be shared. We, as humans, keep making the same mistakes of trying to control ecology only to have it backfire. This is very evident in Hawaii. Time and again people, including those in "responsible" government positions, have brought alien wildlife to the island. The value these introductions were supposed to add quickly degenerated into liabilities. Habitats have been altered bringing subsequent unforeseen problems. These papers reveal a great deal about what not to do. But the people who need the message will not read this publication and if they did they would not understand much of it. The editors need to produce a layman's summary in the style of David Suzuki's latest essays to bring these important results to the politicians and public. No real progress will be made until the consequences of this work reach beyond the scientific community.

ROY JOHN

2193 Emard Crescent, Beacon Hill North, Ottawa, Ontario K1J 6K5 Canada

Global Register of Migratory Species (GROMS): Database, GIS Maps, and Threat Analysis

By K. Riede. 2002. German Federal Agency for Nature Conservation. 404 pages + CD Rom. [in English and German].

Migratory species "...are travellers without passport because they move freely within one world, long before *Homo sapiens* invented political borders, fences, power lines and dams." For the protection of these species across borders the Convention on the Conservation of Migratory Species of Wild Animals, or Bonn Convention, has been initiated.

Arising from this legal situation, GROMS (Global Register of Migratory Species, www.groms.de) was developed. Due to the wealth of information, nicely summarized for so many fascinating and migratory species across the entire animal kingdom, this publication will prove a "pot of gold" for the interested naturalist, conservationist, biologist and wildlife administrator. It also gives an excellent overview and definition of the types of animal migration, and of the applications and use of terms like "threatened" and "endangered". This publication was primarily designed to aid administrative processes; it definitely improves the understanding of migratory species in order to ensure their effective management. GROMS includes a list of 2880 migratory species. A real asset of this publication is that all the names of these species are given in five languages: English, scientific, Spanish, French and German.

Other assets of GROMS, besides an extensive bibliography (in MS ACCESS but not in a common library-database format), are the compiled digital range maps and suggested migration paths for 545 (!) migratory species (divided into Aves, Pisces, Mammalia, and Turtles). These maps are now available in a centralized database and in a common format (e.g., ArcView shape files, GIF). This effort presents an overdue approach that should have been implemented much earlier by the original map providers.

In order to be useful and effective nowadays, science has to deliver digital products with a high scientific standard; e.g., via WWW and for free. The author states from his experience with developing GROMS that "Most of the results are stored on paper or scattered digital resources, not amenable to interactive searching".

Range maps of animals are pretty and please managers and administrators. However, as the author emphasizes nicely, the borderlines in such maps are not absolute but "soft", and may even be seriously misleading. Most of these range maps are based on Minimum Convex Polygon approaches around locations of (museum-) specimen collections or expert opinion, rather than being based on statistically sound approaches with a research design allowing for true inference where animals occur within a certain degree of statistical confidence. In this regard, I thoroughly enjoyed the included HSI (Habitat Suitability Index) approaches in GROMS for African wildlife from the Institute for Applied Ecology.

Of interest in this publication are also the animated (!) flyways and additional GIS datasets, such as islands of the world (although these are presented selectively and some locations deviate by approximately 7 km from my reference maps) and designated RAMSAR sites (spatial error of several kilometers). Banking on the ESRI dataset, which is fully included with the ArcView software, the authors of GROMS also provide the world's rivers, cities, lakes, and country borders.

"This publication contains first results from a global analysis of threat status and a database of migratory mammals, birds, reptiles and fishes. Like other species, migrants suffer from habitat destruction, pollution, overfishing and hunting." As the author states boldly, birds are relatively well known, but for fish, mammals, and insects, information exists only for economically important species. Success in the conservation of migrating animals refers mostly to flagship species, but a silent majority of migratory species and their habitat are continuing to decline unnoticed.

The author and his team worked hard to achieve the provision of a unique (digital) publication of its kind for the global community. Some errors can be forgiven. ArcView is definitely not a "vector-only" GIS but instead has strong raster processing features, and their arguments for using polygon-based maps (e.g., saving hard-drive space) are not convincing. Likely, the focus should be directed towards reliable quality products instead of saving bits and bytes, which became so cheap over the last years. The constant hint in the text that satellite telemetry would be the new and better tool which would allow us to learn where animals (I assume that implies the entire "population") migrate can be questioned, if not rejected. (For cost reasons, most satellite telemetry applications are still based on very few, not representative, samples sizes, preventing valid inferences to a population of thousands of individuals.)

On the technical side, the GROMS CD-ROM worked well on my basic computer; minor bugs are not worthwhile mentioning here. However, GROMS was developed in MS ACCESS "from scratch" and appears sometimes a little clumsy. The stand-alone and specially tailored approach appears somewhat counteractive to the current move of getting databases comparable on a global (software-) standard: e.g., the case for the GROMS Bibliography.

From an international perspective, the strong central European and German influence in GROMS can be irritating. Although GROMS is supposed to deal

with true global ("passport-free") aspects of migratory animals, the national bias is strongly reflected in GROMS's funding, statements, and citations (for instance, the Canadian Bird Banding Atlas is not mentioned, nor the bird migration "bible" by T. Alerstam). Certainly the U.S., nowadays the main player in global conservation issues, is not fully involved or presented in GROMS.

Besides asking in a counter-productive fashion to accept copyrights and other laws when using the CD-ROM version, GROMS makes the strong case for freely accessible and centralized databases on the internet. Unfortunately, GROMS is still too shy in demanding much more effort for such an approach "... it is strange that there is still no 'Birdbase' available". Instead, FishBase (Froese and Pauly 1998, www.fishbase.org, also available on CD-ROM) sets indeed a global example.

Considering that the Bonn Convention — to which needs GROMS eventually caters — is simply an international agreement without any relevant enforcement and that not all countries of the world have even signed, migratory species still have no decent protection. The GROMS Database is a fascinating project with potential to improve this situation. However, it lives in a highly political environment. Fortunately, it has started a new era in which bureaucrats, lawyers, conservationists, naturalists and computer engineers meet (apparently, economists are still not there, yet).

FALK HUETTMANN

Geography Department-Earth Science, 2500 University Drive N.W., University of Calgary, Calgary Alberta T2N 1N4 Canada; E-mail: falk@ucalgary.ca

Carnivore Conservation

Edited by J. L. Gittleman, S. M. Funk, D. MacDonald, and R. K. Wayne. 2001. Cambridge University Press, New York. xiii + 675 pp., illus. Cloth U.S. $41.30; paper U.S. $49.95.

This book takes on the monumental task of assessing the state of current science pertaining to the conservation of carnivores. It is meant for scientists and has not been written for a general audience. The book presents 23 chapters dealing with problems, methods of study, and priorities for conservation and research. Authorship is 60% American and 40% from other nationalities; perhaps a major oversight is the lack of participation of scientists from India, Russia, and China, all of which host many endangered or threatened carnivore species, including virtually all of the global "flagship" species. Most of the work done on carnivores in Canada is omitted.

While there is some dispute about the taxonomy of carnivores, most would agree that the mammalian order Carnivora has at least 10 distinguishable groups, including the well-known canids (dogs) and felids (cats), as well as bears and pandas, weasels, civets, coatis, mongooses, hyenas, walruses, sea lions, and seals. What taxonomic discussion there is revolves around the division between the Viveridae and Herpestidae, and among the Pinnipedia. Nevertheless, the carnivore group is globally highly diverse and comprises a range in size from weasels weighing less than 100 grams to walruses, tigers, and bears weighing many hundred kilograms. As a result, some groups are bound to be given less weight in a general publication such as this, and so if you are interested in aquatic carnivores, viverids, herpestids, procyonids or even the mustelids, then this book will be somewhat disappointing to you. In part this is a result of the body of literature available to the authors, in part because large terrestrial carnivores generally are also threatened species, and in part apparently by authors' choice. In some respects this is unfortunate, as the same examples are cited again and again among the chapters.

Certain of the carnivores are among the most endangered species on the planet, and many others may soon be highly endangered or extinct if human population growth continues unimpeded and reaches the 12 billion predicted for 2050 by the United Nations. The authors point out the many and varying reasons for problem status in many carnivores, including original rarity, low rates of reproduction, island endemism of some, visceral persecution, large space requirements and loss of habitat, and competition with humans for lands occupied by prey species, especially grazing animals. Some carnivores are likely keystone species (not all as suggested in Chapter 11), many are national flagship species, and many likely would make good umbrella or indicator species for environmental change, and yet good research is often lacking.

Books generated from conferences are difficult to develop because ultimately one wants a "story" and not a loose collection of individual papers that could otherwise be published in journals. I did not feel that this was a cohesive book, but the volume offers value nonetheless. The synthesis and writing in several of the chapters are exceptional. In particular, the chapters dealing with extinctions, human-carnivore interactions, re-introductions, genetic concepts, diseases, and setting of conservation priorities are well written, provide broad summaries of the issues and available studies, and reach appropriate conclusions.

While the chapter on dispersal provides a good summary of recent techniques, it should have been improved with a more complete review of the carnivore and theoretical dispersal literature and by attempting to answer the "why disperse?" question. On the other hand, a few of the chapters suffer from being parochial, provide poorly-researched examples, and in one case represents a rehash of the author's previously published personal opinions. While the latter imbalance coupled with certain under-represented groups of carnivores indeed detracts from the capability of the book to achieve its objectives, there is a wealth of information here for scientists. The approximately 2400 references are an important collection, although users must be warned that many are incorrectly cited. Achieving the original goal stated by the editors was almost an impossible task for a subject so varied as carnivores, but the volume provides a good place to start for anyone working with these species.

IAN D. THOMPSON

Canadian Forest Service, Sault Ste. Marie, Ontario P6A 2E5 Canada

Knowing Bass: The Scientific Approach to Catching More Fish

Keith A. Jones. 2002. The Lyons Press, Guilford, Connecticut. vii + 298 pp., illus. U.S. $26.95; $ 40.95.

The stated purpose of this book is to summarize scientific research relevant to the biology of black bass to aid recreational anglers in understanding bass, to help them in turn with capturing bass. Although this is admittedly a very "angler-oriented" book, the author does provide substantial overviews of the life history that may be relevant to naturalists. The author also attempts to provide anglers with knowledge of the factors that contribute to stress and mortality when fish are angled and then released. The book is clearly written for a lay audience, using anecdotes to emphasize points. As a scientist, however, I was somewhat disappointed with the content of the book.

The book has not been peer reviewed and this is clear from several obvious mistakes. For example, the Latin binomial for Smallmouth Bass was changed in 1991 from *Micropterus dolomieui* to *M. dolomieu*, yet the older version of the nomenclature is utilized. Considering that the Smallmouth Bass is one of the focal species of this publication, such an error is surprising. Another example of incomplete or inaccurate information is the explanation of why male bass terminate parental care. The author suggests that this occurs "when the offspring become too active to guard", whereas a more appropriate description would have included comments on the development of predator-avoidance tactics by offspring and the trade-off with regard to parental investment in the current versus future broods (documented by a substantial body of literature). Additionally, slang is used frequently throughout the book (e.g., bedding bass instead of nesting bass). I suspect some of these problems represent oversimplification in an attempt to cater the text to the target audience.

A major deficiency of this work is that the only references present coincide with photographs, figures, or tables that are modified from previously published work. Most of the photographs and generalized line drawings are well done and provide very clear information in support of points being developed by the author. This includes a large number of figures derived from work completed by the author and cited as originating from the Berkley Fish Research data bank. Berkley is arguably the largest player in the improvement of lures and baits and this unique look into their research program is truly informative. Unfortunately, none of these illustrations provide data that are available to the scientific community or sufficient description to determine sample sizes, replicates, and methodology. Some of this information is most interesting (e.g., insect repellents containing deet that come in contact with lures or bait were found to repel bass; the way in which bass respond to different, sizes, colours, scents, etc.) and will definitely be an asset to anglers. Anglers will definitely view these insights into the Berkley research program as the strength of this book.

The portions of the book that focus on feeding biology and sensory biology are the most complete and well done, likely due to the fact that these topics coincide with the expertise of the author. These topics are also of great interest to anglers (although of less interest to the naturalist) concerned with what bass eat, how they eat, and how to make them eat. Coupled with this focus on facilitating capture is a section entitled "Pain and Stress". The discussion on pain is somewhat out of place and detracts from the stress component of the chapter. The discussion on stress is well laid out and focuses both on natural (e.g., predation, hypoxia) and anthropogenic (e.g., angling, livewell retention) stressors. The chapter concludes by reviewing the strategies that can be employed by anglers to minimize stress induced by the actual angling event, air exposure, livewell reten-

tion, and tournament procedures. I found this section to be informative, but not nearly as current as a recent publication from the Bass Anglers Sportsman's Society on the same topic.

My background in science has probably affected my ability to be objective about the content of a book that lacks references. However, if I were a naïve angler, I would likely be quite impressed with the contents. If one purchases the book on the assumption that one will gain a better understanding of bass biology that will aid in the ability to capture more fish, one will likely be satisfied with its contents. This book will find a place on the shelves or in the boats of many bass anglers and does serve as a starting point for those interested in bass biology. Unfortunately, as no references are provided at the conclusion of the text, readers will have little direction for undertaking more detailed investigations. This book is probably of little interest to naturalists, unless one is truly interested in black bass or in a focused, well-illustrated, general discussion of the sensory systems of fish. Despite these shortcomings, it is always difficult to criticize practitioners of science that aid in disseminating technical information to the general public. Even lay contributions, however, could benefit from peer review and some form of bibliography.

STEVEN J. COOKE

Centre for Applied Conservation Research, Department of Forest Sciences, 2424 Main Mall, University of British Columbia, Vancouver, British Columbia V6T 1Z4 Canada

Life Underground, the Biology of Subterranean Rodents

Edited by Eileen A. Lacey, James L. Patton, and Guy N. Cameron. 2000. The University of Chicago Press, Chicago. 449 pp. U.S. $65.00.

This book, edited by Eileen A. Lacey and James L. Patton (University of California, Berkely) and by Guy N. Cameron (University of Cincinnati), is not for readers without a science background, although some of the introductory material is fairly straightforward.

Basically a summary of scientific knowledge regarding subterranean rodent biology, it is divided into three basic parts — Organismal Biology, Population and Community Biology, and Evolutionary Biology — with data organized by topic rather than taxon. Why this organization? Two main reasons. The first, to encourage cross-taxon comparisons needed to address issues of convergence and divergence. The second, to reach a broader audience of biologists, specifically researchers studying similar questions in other groups of organisms; the questions revolve around two basic themes. The first concerns the role of the subterranean niche in shaping the biology of subterranean rodents. The second involves questions about how the properties of the niche have both facilitated and constrained the evolution of the rodents that inhabit it.

The book defines subterranean rodents as "those species that live in underground burrows and that conduct the vast majority of their life activities below the soil surface" and focusses on species that exhibit the greatest restriction to and specialization for life in subterranean habitats. These include mole-voles (family Muridae, subfamily Arvicolinae), zokors (family Muridae, subfamily Myospalacinae), mole-rats (family Muridae, subfamily Spalacinae), bamboo and root rats (family Muridae, subfamily Rhizomyinae), blesmols or African mole-rats (family Bathyergidae), pocket gophers (family Geomyidae), tuco-tucos (family Ctenomyidae), and coruro (family Octodontidae).

Topics of chapters in the Organismal Biology section include morphology, ecophysiological responses to underground habitats, sensory capabilities, communication, and reproduction. The Population and Community Ecology section covers population ecology, community ecology, and spatial and social systems of subterranean rodents. The Evolutionary Biology sections deals with paleontology, phylogenetic patterns, macroevolutionary processes, coevoluton and evolution (a synthesis), and the genetic structure and geography of speciation.

R. SANDER-REGIER

RR5 Shawville, Quebec J0X 2Y0 Canada

Weird Nature: An Astonishing Exploratioin of Nature's Strangest Behavior

By John Downer. 2002. Firefly Books, Willowdale, Ont. 156 pp., illus. Cloth $35; paper $19.95.

If you happen to pick up this book, make sure you have a few hours to spare. Once you start reading, you will find it difficult to put the book down.

Based on a Discovery Channel series of the same name, *Weird Nature* is quick and easy to read, filled with intriguing and surprising facts, and packed full of terrific photographs. In fact, it's difficult to say what takes up more space — photographs or text. So it won't come as a surprise that the information isn't terribly detailed. For this type of book, it doesn't have to be. What matters is the stories it tells, the interest it creates, and the respect it generates for our fellow living beings.

In the six chapters — bearing cute, annoying titles like "Marvelous Motion," "Bizarre Breeding," "Fantastic Feeding," "Devious Defenses"," Puzzling Partners," and "Peculiar Potions" — readers meet all manner of curious wildlife. I'll mention a few examples.

In the "motion" section: flying lizards and snakes, dancing sea slugs, rolling lizards, and those curious jumping beans we've all heard about. In the "breeding" segment: birds with a sense of home decor, male marsupials that mate themselves to death, fish that change gender, and frogs that rear their offspring in their mouths. In the "feeding" part: a shrimp with a sophisticated targeting system, a chameleon with a tongue that moves at ballistic speeds, and fish and a snake that use parts of their bodies as lures to attract prey.

The "defenses" section introduces a flounder able to camouflage itself against a checkerboard pattern, caterpillars that dress themselves in sweaters from wool they have started to eat, an octopus with astounding shape-shifting abilities, and a trio of animals who play dead. The "partners" chapter includes ants that farm food sources, shrimp who provide fish cleaning services, hummingbirds that transport mites, and birds that lead people to honey. Finally, the "potions" segment shows wildlife on drugs, birds that practise aromatherapy, species that use natural insecticides, and pregnant elephants that seek a particular plant to induce birth.

What I really appreciate about this book is its efforts to put this fascinating information into a human context. As the author writes in his introduction, "As we researched the themes of the series and book, it became clear that we were not only uncovering some of the strangest examples of animal behaviour, we were also uncovering something about ourselves.... We think of ourselves as unique — a cut above the other species that inhabit this planet. When that illusion is shattered, we find the comparison strangely disconcerting; the usual reaction is a slightly embarrassed smile."

My reaction was a big grin, admiration for the varied and splendid life forms I was privileged to learn about, and comfort knowing that life beyond our own is strong, ingenious (more than we can imagine), and, I hope, resilient enough to survive the onslaught of our own not-always-so-clever species.

R. SANDER-REGIER

RR5, Shawville, Quebec J0X 2Y0 Canada

The Birds of Heaven: Travels with Cranes

By Peter Matthiessen. Paintings and drawings by Robert Bateman. 2001. Greystone Books, Vancouver 349 pp., illus. $36.95.

If you enjoy a book which includes a world survey of a bird species, off-track travel to find the flocks, and describes the efforts required to monitor them and preserve habitat, this is the book to buy. Peter Matthiessen is a renowned writer, traveller, and naturalist who can turn journeys to find cranes into absorbing adventures, and *Cranes* follows a distinguished list of books which focus on snow leopards, Siberian tigers, and the African veldt, among others. Matthiessen accompanied Dr. George Archibald on expeditions throughout the world to assess the health of crane populations. Dr. Archibald is Chairman of the Board of the International Crane Foundation (ICF) and a hands-on ornithologist. On some other journeys, Matthiessen accompanied Victor Emmanuel, another crane aficionado. The beautiful birds, with their unique calls and graceful displays, make aficionados ("craniacs") of most bird enthusiasts. Of the 15 species world-wide, only two are endemic to North America: the Sandhill and Whooper, and we all know how precarious the population of the latter species is.

In at least one mid-west U.S. state there was (and perhaps still is) a legal hunting season for Sandhills with kill totals of about 100,000 per year! Are they good to eat, or do people really enjoy killing these lovely birds? Despite this, the six races of *Grus canadensis* (Sandhills) are holding their own. For the other 13 species in the rest of the world (all of which Matthiessen has seen in the wild), most are threatened, and constant vigilance is needed to ensure their survival. The exceptions are the two populations of cranes in the Australian Outback (*Grus antigone gilli* (sarus) and *G. rubicundus* (brolga)). Otherwise, dedicated local biologists, with the financial and

physical support of the ICF, monitor threatened species in the Mongolian steppe, Japan, Tibet, India, Africa, and China. Each journey to find a particular species has its own chapter and also describes the anatomy, its breeding requirements, and migration patterns. The illustrations are excellent.

In some East Asian countries cranes are sacred, so there is support by local people to preserve flocks, to the extent of setting up winter feeding stations for "their" cranes. However, expanding cities and polluted marshes and lakes take their toll in many countries.

In many different ways this book will enlighten because "Matthiessen is our greatest modern nature writer in the lyrical tradition" (*New York Times*).

JANE ATKINSON

255 Malcolm Circle, Dorval, Quebec H9S 1T6 Canada

BOTANY

A Flora of Glacier National Park, Montana

By Peter Lesica. 2002. With illustrations by Debbie McNeil. Oregon State University Press, Corvallis, Oregon. 512 pp., illus. U.S. $32.95.

For more than 60 years, I have hiked the trails of Glacier/Waterton Lakes national parks, enjoying the scenic beauty and plant life in this spectacular area. I was excited about reviewing the first new guide to the complete flora of Glacier National Park in more than 80 years. It was not a disappointment.

Lesica starts with an introduction that discusses climate, geology, vegetation zones, history of botanical exploration, floristics, plant geography, methods, and how to use the book. The book's coverage includes 1182 taxa of pteridophytes, gymnosperms, dicots, and monocots. These are all keyed and described, including an 11-page key to the families. There is full treatment of difficult groups, such as willows and grasses.

Artist Debbie McNeil illustrated 351 plants with beautiful and effective black-line drawings. In addition, there are 60 colour photographs by Lesica of plants of grasslands, cold and warm montane forests, wetlands, aspen woodlands, subalpine forests and meadows, and alpine tundra. None are more spectacular than the photograph of bear grass (*Xerophyllum tenax*) on the front cover. Other features of the book include a glossary to help with technical terms, nine pages of up-to-date references, a map, and an index.

My only criticism of the book is the map of Glacier National Park. It does not show Going-to-the Sun Highway, a major feature, or other roads in or near the park. The map indicates that Waterton Lakes National Park is on the northern boundary of Glacier. The presence of Akamina Kishinena Provincial Park on the same boundary is omitted. An additional map showing the distribution of the major vegetation zones within the park would be welcome. Like most books, there are a few gremlins. For example, *Douglasia montana* (page 296) is missing from the index.

This book is a delight and a welcome addition to the flora of the northern Rockies. In combination with *A Flora of Waterton Lakes National Park* (Kuijt 1982), *A Flora of Glacier National Park, Montana* provides this region with the most complete taxonomic coverage of any in the northern Rockies. *A Flora of Glacier National Park, Montana* is a tribute to the author's 20 years of research on the flora. Lesica, McNeil, and Oregon State University Press are to be congratulated on an outstanding publication. If you have any interest in plants, don't go to Glacier without it!

Literature Cited

Kuijt, J. 1982. A flora of Waterton Lakes National Park. University of Alberta Press, Edmonton, Alberta. 684 pages.

GEORGE W. SCOTTER

399 Okaview Road, Kelowna, British Columbia V1W 4K2 Canada

ENVIRONMENT

Bringing the Biosphere Home, Learning to Perceive Global Environmental Change

By Mitchell Thomashow. 2002. The MIT Press, Cambridge, Massachusetts. 244 pp. U.S. $32.95.

It's difficult to say exactly what this book is about. Yes, it's about environmental perception, and learning, and global environmental change. But it's more than that — reflecting Mitchell Thomashow's accumulation of decades of teaching and thinking about the environment and his need to share. Thomashow is Environmental Studies professor at Antioch New England Graduate School.

And so we have this book about perceiving global environmental change, an issue Thomashow admits

he still has trouble coming to grips with. But it is well worth pursuing, because, as he encourages in the first chapter, "Learning about global environmental change is an extraordinary opportunity to study natural history, observe ecosystems, track weather and atmospheric conditions, or to follow the cycling of water and energy through the land, air, and ocean. In so doing, the full splendour of the biosphere is revealed."

Thomashow works through four guiding premises as the book unfolds. The first is what he calls "place-based perceptual ecology," which is basically tuning in to our immediate surroundings and observing and interpreting ecological patterns close to home. The second involves moving beyond our immediate surroundings and exploring the relationships between places. The third premise explores further relationships regarding the spatial and temporal dimensions of environmental change. And the fourth deals with interconnected learning pathways: natural history and local ecology, the life of the imagination, and spiritual deliberation.

It may appear highly theoretical, and it is. Yet the book is well written and engaging, full of enthusiasm, and densely packed with information (and some jargon). The frequent sub-titles help to break up the text and organize the information for readers, but sometimes it still left my head spinning, so I would recommend reading it in little chunks.

What I really appreciated about this book was its conversational tone, the personal narrative interwoven with theory, the interdisciplinary nature of the information, and the references to other authors and books (which I've noted and intend to look up). Teachers involved in studies relating to environmental topics and naturalists interested in widening the scope of their personal inquiry would find this book a worthwhile read.

R. SANDER-REGIER

RR5, Shawville, Quebec J0X 2Y0 Canada

Trees, Shrubs, and Vines for Attracting Birds

By Richard M. DeGraaf. 2002. 2nd revised edition. University of New England Press, Lebanon, New Hampshire. xiii + 169 pp., illus. U.S. $19.95.

Having just moved to a new place with a fair bit of open pasture land, I immediately thought of planting for aesthetics as well as visual and wind barriers. Being a wildlife biologist, I also considered the usefulness of these plantings for attracting birds and other wildlife. This book arrived soon after the move and so I decided to read it and plan my plantings with a little professional advice. This decision resulted in an enjoyable and informative read.

This is a revised version of a 1979 publication. It claims to be significantly updated, with many recent field notes included. Out of three pages of references, only two flora publications postdated 1979. Although an American publication, the book covers Canada equally well, both in the written discussions and the hardiness map. Although the preface says data are provided on 162 species of plants, I found only 137 — 61 trees, 67 shrubs, and 9 vines.

The introduction provides valuable insights into planning, landscaping, and long-term considerations to be made prior to planting. One must consider attractiveness to people versus attraction to birds, as these are not always mutual. Some ornamentals, such as forsythias and hydrangeas, or trees such as eastern redbud are rarely used by birds. Some plants are invasive and should not be introduced to a limited area urban site or to rural locations. One has to consider the mature size of the species, the uses of surrounding lands, and building sites when planning. A good landscaping plan of the area is recommended.

The species of vegetation are arranged by alphabetic species name under three chapters, one each for trees, shrubs, and vines. Each species is given between half and $1^1/_2$ pages of text. Many have excellent black-and-white line drawings and some black-and-white photographs. Each species is described under common and species names, family, a general description, range and hardiness, landscaping notes, propagation notes, and a table indicating the species of birds which use the plant and for what purpose (food, cover, or nesting). I was interested to find that 33 species of birds use poison ivy (berries as food), but this has not convinced me to plant it in my yard.

The book is completed by four informative appendices, including the hardiness zones map, growth and fruiting period table, precautions on invasive species, and plants recommended for specific growth conditions. There are also three pages of references, two pages of glossary, and an index.

I recommend the book highly for anyone who wants to plant and enjoys birds.

WILSON EEDY

Terfa Inc, RR# 1 Glencairn, Ontario L0M 1K0 Canada

NEW TITLES

Zoology

Arte de pajaros/ Art of birds. 2003. By P. Neruda, translated by J. Schmitt. Lynx Edicions, Barcelona. 208 pp., illus. U.S.$ 22.50.

Birds of North America. 2002. By F.J. Allsop III. DK Publishing, New York. 1008 pp., illus. U.S.$ 60.

Birds of Oregon: a general reference. 2003. Edited by D.B. Contreras. Oregon State University Press, Corvallis. 704 pp., illus. U.S.$ 65.

*__Birds of the Saskatoon area__. 2002. Edited by A.L. Leighton, J. Hay, C.S. Houston, J.F. Roy, and S. Shadick. Special Publication 23. Saskatchewan Natural History Society, Regina. 345 pp., illus. $39.

*__Birds of the untamed west: the history of birdlife in Nebraska, 1750 to 1875__. 2000. By J.E. Ducey. Making History, Omaha, Nebraska. 300 pp., illus. U.S.$ 25.

Birds of the Yukon Territory. 2003. Edited by P.H. Sinclair, W.A. Nixon, C.D. Eckert, and N.L. Hughes. UBC Press, Vancouver. 604 pp., illus. $125.

Bugs of Ontario. 2003. By J. Acorn and I. Sheldon. Lone Pine, Edmonton. 160 pp., illus. $14.95.

*__Caviar: the strange history and uncertain future of the world's most coveted delicacy__. 2002. By I. Saffron. Broadway Books, New York. xv + 570 pp. U.S.$ 35.95.

†__Crabs in cold water regions: biology, management, and economics__. 2002. Edited by A.J. Paul, *et al.* Alaska Sea Grant Program, University of Alaska, Fairbanks. x + 866 pp., illus. U.S.$ 40.

*__The complete guide to Antarctic wildlife__. 2002. By H. Shirihai. Princeton University Press, Princeton. 510 pp., illus. U.S.$ 49.50.

*__The dinosaur filmography__. 2002. By M.F. Berry. McFarland, Jefferson, North Carolina. 483 pp., Illus. U.S.$ 65.

Endangered animals. 2002. Edited by S. Barrington and J. Newson. Grolier, Danbury, Connecticut. 10 volumes, each 112 pp., illus. Set U.S.$ 409.

†__Exploring animal behavior in laboratory and field: a hypothesis-testing approach to the development, causation, function, and evolution of animal behavior__. 2003. Edited by B.J. Ploger and K. Yasukawa. Elsevier Science, Burlington, Massachusetts. xix + 472 pp., illus.

Field guide to fishes: North America. 2002. By C.R. Gilbert and J.D. Williams. Knopf, New York. 607 pp., illus. U.S.$ 19.95.

Fish of Alberta. 2003. By M. Sullivan and A. Joynt. Lone Pine, Edmonton. 176 pp., illus. $17.95.

†__Great wildlife of the Great Plains__. 2003. By P.A. Johnsgard. University Press of Kansas, Lawrence. xv + 309 pp., illus. U.S.$ 29.95.

*__Guide to the reptiles of the eastern Palearctic__. 2003. By N. Szczerbak. Krieger Publishing, Melbourne, Florida. 350 pp., illus. U.S.$ 73.50.

†__Invertebrates__. 2003. By R.C. Brusca and G.J. Brusca. 2nd edition. Sinauer Associates, Sunderland, Massachusetts. xxx + 936 pp., illus. U.S.$ 109.95.

†__The life of mammals__. 2002. By D. Attenborough. Princeton University Press, Princeton. 320 pp., illus U.S.$ 29.95.

Jungle bugs: masters of camouflage and mimicry. 2003. By B. Purser. Firefly Books, Willowdale, Ontario. 144 pp., illus. $19.95.

*__Mammals of Ontario__. 2002. By T. Eder. Lone Pine, Edmonton. 215 pp., illus. $24.95.

†__A passion for wildlife: the history of the Canadian Wildlife Service__. 2003. By J.A. Burnett. UBC Press, Vancouver. xiii + 331 pp., illus. Cloth $85; paper $27.95.

*__The rockfish of the northeastern Pacific__. 2002. By M.S. Love, M. Yoklavich, and L. Thorsteinson. University of California Press, Berkeley. x + 405 pp.

Sleep and rest in animals. 2003. By C. Lacrampe. Firefly Books, Willowdale, Ontario. 112 pp., illus. $24.95.

†__Sparrows and finches of the Great Lakes Region and eastern North America__. 2003. By C. Earley. Firefly Books, Willowdale, Ontario. 128 pp., illus. Cloth $24.95; paper $16.95.

†__Stonechats: a guide to the genus *Saxicola*__. 2002. By E. Urquhart. Yale University Press, New Haven. 320 pp., illus. U.S.$ 60.

Tarantulas of Belize. 2003. By S.R. Reichling. Krieger Publishing, Melbourne, Florida. 248 pp., illus. Cloth U.S.$ 29.50; paper U.S.$ 21.95.

†__Warblers of the Great Lakes Region and eastern North America__. 2003. By C. Earley. Firefly Books, Willowdale, Ontario. 128 pp., illus.Cloth $24.95; paper $16.95.

Wildlife responses to climate change: North American case studies. 2002. Edited by S.H. Schneider and T.L. Root. Island Press, Washington. 437 pp., illus. U.S.$ 60.

†__What good are bugs: insects in the web of life__. 2003. By G. Waldbauer. Harvard University Press, Cambridge, Massachusetts. 366 pp., illus.

Botany

†__Alberta wayside wildflowers__. 2003. By L. Kershaw. Lone Pine, Edmonton. 160 pp., illus. $16.95.

Cultivated and native asters of Ontario. 2002. By J.C. Semple, S.B. Heard, and L. Brouillet. University of Waterloo, Biology Department, Waterloo, Ontario. 134 pp., illus. $28.

Gathering moss: a natural and cultural history of mosses. 2003. By R.W. Kimmerer. Oregon State University Press, Corvallis. 176 pp., illus. U.S.$ 17.95.

The genus *Arisaema*: a monograph for botanists and nature lovers. 2003. By G. Gusman and L. Gusman. Timber Press, Portland, Oregon. c450 pp., illus. U.S.$ 69.95.

†**Manitoba wayside wildflowers**. 2003. By L. Kershaw. Lone Pine, Edmonton. 160 pp., illus. $16.95.

†**Saskatchewan wayside wildflowers**. 2003. By L. Kershaw. Lone Pine, Edmonton. 160 pp., illus. $16.95.

Trees of the Carolinian forest: a guide to species, their ecology, and uses. 2003. By G. Waldron. Boston Mills Press, Erin, Ontario. 288 pp., illus. $24.95.

Environment

Biomes and habitats. 2002. By P. Whitfield, P.D. Moore, and B. Cox. Macmillan, New York. 220 pp., illus. U.S.$ 95.

*__Books and the sciences in history__. 2000. Edited by M. Frasca-Spada and N. Jardine. Cambridge University Press, New York. xiv + 438 pp., illus. U.S.$ 32.

Britain: traveller's nature guide. 2003. By M. Walters and B. Gibbons. Oxford University Press, Don Mills, Ontario. 320 pp., illus. $35.95.

Caught in fading light: mountain-lions, zen masters, and wild nature. 2003. By G. Thorp. Greystone Books, Douglas and McIntyre, Vancouver. 208 pp. $29.95.

A citizen's guide to ecology. 2003. By L.B. Slobodkin. Oxford University Press, Don Mills, Ontario. 254 pp. $25.50.

*__City wilds: essays and stories about urban nature__. 2002. Edited by T.F. Dixon. University of Georgia Press, Athens. xviii + 311 pp. Cloth U.S.$ 45; paper U.S.$ 19.95.

A desert calling: life in a forbidden landscape. 2002. By A.A. Mares. Harvard University Press, Cambridge, Massachusetts. xvii + 318 pp., illus. U.S.$ 29.95.

†__Diary of a lake__. 2002. Edited by J. Harris and V. Lougheed. Books and Company, Prince George, British Columbia. 213 pp., illus.

The earth's biosphere. 2002. By V. Smil. MIT Press, Cambridge, Massachusetts. 346 pp., illus. U.S.$ 32.95.

France: travellers' nature guide. 2003. By B. Gibbons. Oxford University Press, Don Mills, Ontario. 320 pp., illus. $35.95.

Global warming: cause, effects, and the future. 2002. By M. Maslin. Voyageur, Stillwater, Maine. 72 pp., illus. U.S.$ 16.95.

Greece: travellers' nature guide. 2003. By B. Gibbons and M. Walters. Oxford University Press, Don Mills, Ontario. 320 pp., illus. $35.95.

Life lessons from the environmental edge: volume 1, the hunt of a lifetime; volume 2, laugh at yourself for others surely will; and volume 3, people and politics. Environmental Edge, Simpsonville, North Carolina. 14 pp., illus; 13 pp., illus.; and 12 pp., illus. Free at www.edgestuff.com as Adobe pdf files.

†__Macroevolutionary theory on macroecological patterns__. 2003. By P.W. Price. Cambridge University Press, New York. x + 291 pp., illus. Cloth U.S.$ 85; paper U.S.$ 30.

*__Monteverde: ecology and conservation of a tropical cloud forest__. 2000. Edited by N.M. Nadkarni and N.T. Wheelwright. Oxford University Press, Don Mills, Ontario. xiii + 573 pp., illus. $43.95.

†__Natural grace: the charm, wonder, and lessons of Pacific northwest animals and plants__. 2003. By W. Dietrich. University of Washington Press, Seattle. 236 pp., illus. U.S.$ 16.95.

Nature by design: people, natural process, and ecological restoration. 2003. By E. Higgs. MIT Press, Washington. 416 pp., illus. Cloth U.S.$ 68; paper U.S.$ 27.95.

Paradise wild: reimaging American nature. 2003. By D. Oates. Oregon State University Press, Corvallis. 320 pp. U.S.$ 21.95.

*__Plundering paradise: the hand of man on the Galapagos Islands__. 2002. By M. d'Orso. Harper Collins, New York. xix + 345 pp., illus. U.S.$ 24.95.

Rainforest. 2003. By S. Oldfield. MIT Press, Washington. 160 pp., illus. U.S.$ 29.95.

*__Remote sensing for sustainable forest management__. 2001. By S.E. Franklin. Lewis Publications, Boca Raton, Florida. 407 pp. U.S.$ 99.95.

The saltwater wilderness. 2003. By G. Vanstrum. Oxford University Press, Don Mills, Ontario. 304 pp., illus. $34.95.

Spain: travellers' nature guide. 2003. By T. Farino and M. Lockwood. Oxford University Press, Don Mills, Ontario. 500 pp., illus. $35.95.

*__A spring expedition to the Falkland Islands and Antarctic__. 2001. By D.L. Knott. Masalavita Video Productions, West Linn, Oregon. Video.

State of the world. 2002. By Worldwatch Institute, Norton, New York. 265 pp., illus. U.S.$ 29.95.

***Visions of the land: science, literature, and the American environment from the era of exploration to the age of ecology**. 2002. By M.A. Bryson. University of Virginia Press, Charlottesville. xvii + 228 pp. Cloth U.S.$ 45; paper U.S.$ 16.50.

***The war on weeds in the prairie west: an environmental history**. 2002. By C.L. Evans. University of Calgary Press, Calgary. xvi i + 309 pp.

Wild Earth: wild ideas for a world out of balance. 2002. Edited by T. Butler. Milkweed, Minneapolis. xxi + 334 pp. U.S.$ 18.95.

Win-win ecology: how the Earth's species can survive in the midst of human enterprise. 2003. By M. Rosenzweig. Oxford University Press, Don Mills, Ontario. 240 pp., illus. $45.

Miscellaneous

†Good news for a change: how everyday people are helping the planet. 2003. By D. Suzuki and H. Dressel. Greystone Press, Douglas and McIntyre Publishing, Vancouver. 399 pp. $24.95.

†Hiker Mike: adventures farther afield. 2003. By M. Kirby. Boston Mills Press, Toronto. 176 pp., illus. $19.95.

***John Keast Lord: materials for a life**. 2002. By D. Baker. Backhays Publishers, Leiden, Netherlands. 78 pp., illus. Euro 22.

†A journal of visits to Hawaii by William W. and Kathryn E. Judd, 1976-1987, with an account of birds seen in the islands. 2003. By W.W. Judd. Phelps Publishing, London, Ontario. 110 pp., illus. $10.

†Life on air: memoirs of a broadcaster. 2002. By D. Attenborough. Princeton University Press, Princeton. 384 pp., illus. U.S.$ 29.95.

†Record of documents, 1969 – 2002, pertaining to the preservation of Reservoir Hill, London, Ontario. 2003. By W.W. Judd. Phelps Publishing, London, Ontario. 81 pp., illus. $8.

†Snowshoes and spotted dick: letters from a wilderness dweller. 2003. By C. Czajkowski. Harbour Publishing, Madeira Park, British Columbia. 304 pp., illus. $24.95.

Books for Young Naturalists

Animals of the coral reef under the sea. 2002. By L.M. Stone. Rourke Publishing, Vero Beach. 24 pp., illus. U.S.$ 18.60.

Animal talk. 2002. By M. McDaniel. Benchmark Books, Tarrytown, New York. 32 pp., illus. U.S.$ 14.95.

Cricketology. 2002. By M.E. Ross. Lerner, Minneapolis. 48 pp., illus. U.S.$ 19.95.

Hibernation. 2002. By C. Scrace. Franklin Watts, Danbury, Connecticut. 32 pp., illus. U.S.$ 24.

Ladybugs: red, fiery, and bright. 2002. By M. Posada. Carolrhoda, Minneapolis. 32 pp., illus. 32 pp., illus. U.S.$ 15.95.

Let's find it! My first nature guide. 2002. By K. Arnold. Holiday House, New York. 32 pp., illus U.S.$ 16.95.

The life cycle of a bird. 2002. By B. Kalman and K. Smithyman. Crabtree, New York. 32 pp., illus. U.S.$ 15.95.

The life cycle of a frog. 2002. By B. Kalman and K. Smithyman. Crabtree, New York. 32 pp., illus. U.S.$ 15.95.

Mammoths: ice-age giants. 2002. By L.D. Agenbroad and L. Nelson. Lerner, Minneapolis. 120 pp., illus. U.S.$ 26.60.

Pond life. 2002. By D. Stewart and M. Bergin. Franklin Watts, Danbury, Connecticut. 32 pp., illus. U.S.$ 24.

Salmon forest. 2003. By D. Suzuki and S. Ellis. Greystone Books, Douglas and McIntyre, Vancouver. 32 pp., illus. $18.95.

Take an ecowalk to explore science concepts, grades 1 – 5. 2002. By S. Szeto. Trifolium, Toronto. v + 90 pp., illus. $18.95.

1,001 facts about dinosaurs. 2002. By N. Clark and W. Lindsay. DK Publishing, New York. 192 pp., illus. U.S.$ 8.95.

1,001 facts about sharks. 2002. By J. Pope. DK Publishing, New York. 192 pp., illus. U.S.$ 8.95.

Tigers. 2002. By E. Watt. Raintree, Austin, Texas. 64 pp., illus. U.S.$ 18.98.

* Assigned for review
† Available for review

News and Comment

Amphipacifica: Journal of Aquatic Systematic Biology 3(3)

Volume 3, Number 3 (134 pages) was issued 15 November 2002. It contains: The talitroidean amphipod genus *Hyale* Rathke, 1837, sens. str. in the North Atlantic and Mediterranean regions: T. Krapp-Schickel and E. L. Bousfield — Corrections to Amphipacifica, Volume 3, Numbers 1 & 2 — Feature Article: The talitroidean amphipod family Hyalidae revised, with emphasis on the North Pacific fauna: systematics and distributional ecology: E. L. Bousfield and E. A. Hendrycks.

The new taxa of amphipods in the 11 full issues of *Amphipacifica* totalling 1466 pages published since January 1994 (excluding a 25-page supplement dealing exclusively with presumptive vertebrate *Cadborosaurus willsi*, new genus, new species). The total number of new amphipod taxa is 233, encompassing 17 new subfamilies, 43 new genera, 10 new subgenera, 162 new species and 1 new subspecies, an average of about 1 new taxon for every six pages. The species total as a percentage of described North American and world species is approximately 10% and 2.3%, respectively. These 11 issues also fully treat (redescribe, refigure and key) more than 150 species previously named by others (including many new Canadian records) and contain three major amphipod papers that are mostly phyletic and North American regional faunistic in nature in which no new taxa were described. They also contain a paper on Cambrian aquatic arthropods in which 4 new subclasses and 3 new orders were proposed, and a paper on Caribbean decapod shrimps in which 3 new species were described (Analysis provided by ELB).

Subscription rate is $12.50 (CAN) per issue. The cost of back numbers is negotiable, depending on postal rates. Please address all correspondence to: Edward L. Bousfield, Managing Editor, Amphipacifica Research Publications, 1710-1275 Richmond Road, Ottawa, Ontario K2B 8E3 Canada. e-mail: elbousf@magma.ca

Froglog: Newsletter of the Declining Amphibian Populations Task Force (54 and 55)

Number 54, December 2002. Contents: New Zealand Frog Week (Phil Bishop) — Chytridiomycosis in Northern and Western Cape frog populations (Samantha Hopkins and Alan Channing) — Global Amphibian Assessment Makes Rapid Progress (Simon Stuart) — First Records of Organochlorine Pesticide Residues in Amphibians of Mesopotamic Region, Argentina (R. Lajmanovich, E. Lorenzatti, P. de la Sierra, F. Marino, and P. Peltzer) — Amphibian Decline in Israel — A New Research Project (Avital Gasith) — EU Takes Note of Atrazine Research [Atrazine Levels Threaten Frog Populations *[reproduced with kind permission from Pesticide News (2002) 57: 16]* (Roslyn McKendry) — Froglog Shorts — Instructions for Contributors. [Note Publications of Interest no longer included due to their steadily increasing rate. This list updated monthly is available at website: http://www.open.ac.uk/daptf/index.htm].

Number 55, February 2003. Contents: The Himalayan Newt (*Tylototriton verrucosus*), an Endangered Species of India (Daniele Seglie and Debjani Roy) — Pathogens and Amphibian Declines (James P. Collins; see http://life-sciences.asu.edu/irceb/amphibians) — Zimbabwe's Fast Track Land Re-settlement and its Impact on Amphibians (from a correspondent in Zimbabwe) — Adaptive Cluster Sampling for Amphibians (Lee-Ann C. Hayek and Ron Heyer) — USGS Press Release, 3 December 2002: Shedding Light on Amphibian Declines: New Research Finds That Ultraviolet Radiation May Not be a Factor in Amphibian Population Declines — Froglog Shorts: Donations.

Publication of issues 54 and 55 were supported by Peace Frogs (www.peacefrogs.com) and by RANA and the U.S. National Science Foundation grant DEB-0130273.

Froglog is the bi-monthly newsletter of the Declining Amphibian Populations Task Force of The World Conservation Union (IUCN)/Species Survival Commission (SSC) and is supported by The Open University, the World Congress of Herpetology, and Harvard University. The newsletter is Edited by John W. Wilkinson, Department of Biological Sciences, The Open University, Walton Hall, Milton Keynes, MK7 6AA United Kingdom; e-mail: daptf@open.ac.uk. Funding for *Froglog* is underwritten by the Detroit Zoological Institute, P. O. Box 39, Royal Oak, Michigan 48068-0039, USA.

Point Pelee Natural History News 2(4)

The winter 2002 issue, volume 2, pages 53-64, contains: Another Cave Swallow Invasion: The Fall of 2002 (Alan Wormington); Noteworthy Bird Records: September to November 2002 (Alan Wormington); Vermilion Flycatcher: New to Point Pelee (David R. Don); Mid-Winter Birding at Point Pelee: In Search of Water (Alan Wormington) — In the Field — Point Pelee Christmas Bird Count: December 16, 2002 (Sarah Rupert).

This newsletter for Point Pelee National Park, Ontario, is published by the Friends of Point Pelee and edited by Alan Wormington (e-mail: wormington@juno.com). Editorial Assistants are Marilyn R. Scase and Matthew J. Smith. The web site is www.wincom.net/~fopp/Natural_History_News.htm. Subscription rates are Canada: CAN $15 (one year) or $30 (two years); International: US $15 (one year) or $30 (two years). Send payment (and e-mail address, optional) to The Friends of Point Pelee, 1118 Point Pelee Drive, Leamington, Ontario N8H 3V4 Canada. Issues are mailed in March, June, September, and December, and back issues are available for $15 per Volume/ $5 per issue (postage paid).

Curatorial Reports on Natural History Topics: Nova Scotia Museum of Natural History

The Curatorial Reports of the Nova Scotia Museum make technical information on museum collections, programs, procedures and research accessible to interested readers. The reports may be cited in publications, but their manuscript status should be clearly indicated.

The following list of Curatorial Reports was revised by John Gilhen, 22 December 2002.

(1) Scott, Fred. 1967. Catalogue of the ornithological collections of the Nova Scotia Museum. 53 pages.
(2) Gilhen, John. 1968. Catalogue of marine crustacea in the Nova Scotia Museum. 12 pages.
(3) Gilhen, John. 1969. The fish collections of the Nova Scotia Museum. 43 pages.
(4) Scott, Fred and Barry Wright. 1972. Shrews, moles and myomorph rodents in the Nova Scotia Museum collection. 9 pages.
(5) Wright, Barry and Ken Neil. 1972. Sphinx moths in the Nova Scotia Museum Collection (Lepidoptera-Sphingidae). 32 pages.
(6) Scott, Fred and Barry Wright. 1972. The small mammal survey 1971. 40 pages.
(7) Malcolm, Pamela. 1972. A preliminary survey of the cancrid crabs in Nova Scotia coastal waters. 20 pages.
(8) Grigg, Ursula. 1972. Freshwater mussels in the Nova Scotia Museum collection. 18 pages.
(9) Davis, Derek S. 1973. Notes on a collection of specimens made by the Challenger Expedition 1873. 12 pages.
(10) Davis, Derek S. and John Gilhen. 1973. Marine animals collected during FRB cruise 104 1972. 5 pages.
(11) McClung, R. Paul. 1974. Leeches of the St. Mary's River watershed and leech records of the Nova Scotia Museum. 15 pages.
(12) Doleman, Paul S. 1973. Collections made in association with *C. S. S. Dawson* cruise 72–004. 19 pages.
(13) Doleman, Paul S. 1973. Collections made in association with *C. S. S. Hudson* cruise 73–002. 13 pages.
(14) McClung, Paul. 1973. An analysis of three samples of whelks from Nova Scotia waters. 13 pages.
(15) Barnes, Robert. 1973. Bats in the Nova Scotia Museum collection. 4 pages.
(16) McDonald, John. 1973. A catalogue of the A. H. MacKay lichen collection with a short biography of A. H. MacKay. 13 pages.
(22) Gilhen, John. 1974. Distribution, natural history and morphology of the blue-spotted salamanders *Ambystoma laterale* and *A. tremblayi* in Nova Scotia. 38 pages.
(24) Davis, D. S. and John Gilhen. 1974. A collection of animals from Shelburne Harbour, 1973. 6 pages.
(27) Harvey, Mary MacKay. 1975. Gardens of Shelburne, Nova Scotia, 1785-1820. 45 pages.
(30) Scott, Fred and Barry Wright. 1975. Catalogue of the ornithological collections of the Nova Scotia Museum. 50 pages.
(31) Davis, Derek S. 1976. Benthic animals from Cruises P. 114 and P. 139, 1973 and 1974. 23 pages.
(32) Aldous, Don. 1976. Decapod crustaceans in the Nova Scotia Museum collection. 34 pages.
(33) MacAlaster, Elizabeth. 1977. Cephalopods in the Nova Scotia Museum collection. 26 pages.
(34) Davis, Derek S. 1976. The estuary of the St. Mary's River, Nova Scotia 1973. 23 pages.
(35) Science Section Staff. 1978. The Wight Nature Preserve, Hubbards, Nova Scotia. 36 pages.
(36) Wright, B. 1979. Nova Scotian flees. 21 pages.
(37) Davis, D. S. and Alex Wilson. 1979. Notes on the flora and fauna of six lakes in Cape Breton Highlands National Park. 41 pages.
(38) Scott, Fred. 1979. Preliminary investigations at Hayes Cave, Hants County, Nova Scotia, in 1978. 14 pages.
(40) Davis, Derek S. 1979. The Cole Harbour Heritage Farm parkland. 31 pages.
(41) LeBlanc, Jan. M. and R. Paul McClung. 1979. Leech (Hirudinoidea) records for the province of Nova Scotia. 27 pages.
(42) Ogilvie, Robert. 1979. The mineralogy collection: operation manual and state of the collection. 33 pages.
(43) Pocklington, Patricia. 1979. Polychaetous annelids in the Nova Scotia Museum collection. 52 pages.
(44) Davis, Derek S. 1981. Aquatic fauna of the Shubenacadie head-water lakes: an exercise in information retrieval. 15 pages.
(45) Gilhen, John and Fred Scott. 1981. Distributions, habitats and vulnerability of amphibians, reptiles, and small mammals in Nova Scotia. 21 pages.
(46) Isnor, Wendy. 1981. Provisional notes on the rare and endangered plants and animals of Nova Scotia. 105 pages.
(49) Ogilvie, Robert. 1984. Important ecological sites in Nova Scotia. 34 pages.
(50) Morris, Linda. 1985. The Hayes Cave site South Maitland. 128 pages.
(51) Grantham, Robert G. 1985. Index of the Nova Scotia Museum mineral collection. 52 pages.
(52) Grantham, Robert G. 1985. Index of the Nova Scotia Museum economic minerals collection. 19 pages.
(53) Grigg, Ursula. 1985. An introduction to the Cenozoic Ostracoda (Crustacea) of Arctic and Eastern Canada. 13 pages.
(54) Davis, Derek S. 1985. Synopsis and distribution tables of land and freshwater mollusca of Nova Scotia. 30 pages.
(56) Katz, Geoffrey E. 1986. Planning for ecological reserves in Nova Scotia. 90 pages.
(68) Wright, Barry. 1989. The fauna of Sable Island. 93 pages.
(78) Pronych, Gilda and Alex Wilson. 1993. Atlas of rare vascular plants in Nova Scotia. 2 Volumes: 331 (1:168, 2:163) pages.
(79) Browne, Susan. 1994. Frogwatch 94: program development and results. 75 pages.
(86) Moseley, Max. 1998. Invertebrate fauna of Nova Scotia caves. 39 pages.
(89) Gilhen, John. 1999. Fishes of Nova Scotia: Species recorded in the accession books of Harry Piers from 1899 to 1939. 153 pages, 107 plates.
(90) Natural History Section Staff. 2000. The Nova Scotia Museum Isle Haute Expedition, July 1997. 53 pages.
(96) Rojo, Alfonso L. 2002. Morphological and biometric study of the bones of the buccal apparatus of some Nova Scotia fishes of archaeolgical interest. 183 pages.

Toll free order & information line: 1-800-632-1114
Halifax metro: 424-7344
Fax: 1-902-424-0560
e-mail: nsmbooks@gov.ns.ca
Postal mail: Nova Scotia Museum, Heritage Resources Services, 1747 Summer Street, Halifax, Nova Scotia B3H 3A6 Canada

Canadian Species at Risk November 2002

Issued by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) the list is 38 pages containing: About COSEWIC (mandate, membership, definitions); — Summary Tables (COSEWIC species at risk, not at risk, and data deficient; results of May 2002 COSEWIC meeting), COSEWIC Lists (Explanation of symbols, Geographical occurrence and abbreviations; List 1. Species designated in the five "risk" categories; List 2. Species examined and designated in the not at risk category; List 3. Species examined and designated in the data deficient category) — Record of Status Re-examinations — List of name changes — COSEWIC Species Specialist and Aboriginal Traditional Knowledge Subcommittee Contacts (2002-2003). Listed now are 12 extinct, 21 extirpated, 141 endangered, 99 threatened, and 142 of special concern. Of the 415 forms in these categories, 63 are mammals, 56 birds, 30 reptiles, 19 amphibians, 77 fishes, 11 lepidopterans, 14 molluscs, 132 vascular plants, 7 mossses, and 6 lichens. In addition, 146 forms have been considered and found not at risk, and 28 to be data deficient.

This publication is available from COSEWIC Secretariat, c/o Canadian Wildlife Service, Environment Canada, Ottawa, Ontario K1A 0H3. See Web site: www.cosewic.gc.ca.

Amphibian Voice Winter 2002

Volume 12, Number 4, is 8 pages and contains — Frogwatch-Ontario, Frogwatch-Canada: Answering the Call [Elizabeth Kilvert, Monitoring & Assessment Network (EMAN) Coordinating Office] — Frogwatch-Ontario: A Regional Perspective [Phung Tran] — Why Watch Frogs? [Phung Tran] — Lily Pads & Cattails: 2002 Frogwatch Program [Sarah Ingwersen] — Frogwatching for Dummies: A Guide to Monitoring with Frogwatch-Ontario — How to Monitor with Frogwatch-Ontario — Ribbet's Review [Phung Tran] — Call'um of the Wild: Diary of a Frogwatcher [Barbara Pratt].

Amphibian Voice is edited by Sarah Ingwersen, Adopt-A-Pond Coordinator, and Bob Johnson, Curator of Reptiles and Amphibians, Toronto Zoo, and is distributed to schools and communities participating in the Adopt-a-Pond programme. It is published with support of the Toronto Zoo Foundation, HRDC, Young Canada Works and is a non-profit wetland education programme, funded by grants and private donations.

For copies, to participate, and/or to make donations, contact Adopt-A-Pond, Toronto Zoo, 361A Old Finch Avenue, Scarborough, Ontario M1B 5K7; Fax: (416)-392-4979; e-mail: aap@torontozoo.ca. Web site: www.torontozoo.com/adoptapond.

Marine Turtle Newsletter (99)

January 2003. 40 pages. Contents — OBITUARY: John Roscoe Hendrickson 1921-2002 — EDITORIAL: Living Tag, Living Reputation — ARTICLES: A Conservation Success: Leatherback Turtles in the British Virgin Islands — Epibiots of Hawksbill Turtles *Eretmochelys imbricata* in a Caribbean Nesting Ground: A Potentially Unique Association with Snapping Shrimp (Crustacea: Alpheidae) — Predation on Loggerhead and Leatherback Post-Hatchlings by Gray Snapper — Marine Turtle Conservation Initiatives at Ras Laffan Industrial City, Qatar (Arabian Gulf) — The Surf Crab (*Arenaeus cribrarius*): A Predator and Prey Item of Sea Turtles — NOTES: First Record of Juvenile Leatherback Stranding in Mona Island, Puerto Rico — Juvenile Green Turtle Tagged in Florida Recorded at Tortuguero, Costa Rica — First Record of Olive Ridley Nesting in the State of Ceara, Brazil — BOOK REVIEWS — ANNOUNCEMENTS — NEWS & LEGAL BRIEFS — RECENT PUBLICATIONS.

The Marine Turtle Newsletter is edited by Brendan J. Godley and Annette C. Broderick, Marine Turtle Research Group, School of Biological Sciences, University of Wales, Swansea, SA2 8PP Wales, United Kingdom; e-mail MTN@swan.ac.uk; Fax +44 1792 295447. Subscriptions to the MTN and donations towards the production of MTN and its Spanish edition NTM [Noticiero de Tortugas Marinas] should be sent to Marine Turtle Newsletter c/o Chelonian Research Foundation, 168 Goodrich Street, Lunenburg, Massachusetts 01462 USA; e-mail RhodinCRF@aol.com; Fax + 1 978 582 6279. MTN website is: www.seaturtle.org/mtn//.

Recovery: An Endangered Species Newsletter (23)

The February 2003 issue contains: RECOVERY HIGHLIGHTS: Re-routing lanes; Fish ladder a success; Amphibian tunnels constructed; PROFILE: In memoriam: Wayne Harris; NEWS BITES: Managing grizzlies; Strategy in development [Blunt-lobed Woodsia, *Woodsia obtusa*]; Conserving birds [Douglas Marsh, east of Brandon]; Blue-flag recovery - a cooperative approach; COSEWIC Update; RENEW Update; Legislative Update: SARA given royal assent [*Species at Risk Act* 12 December 2002]; Polar Bear Act [Manitoba]; New species protected [Nova Scotia: 4 added for total of 20]; Special Protection [Newfoundland and Labrador Endangered Species Act covers 20 species considered endagered, threatened, or vulnerable]: FIELD NOTES: Recovering the Eastern Fox Snake [Ontario: Angela Coxon]; Conserving limestone barrens [Newfoundland: Douglas Ballam]; Mapping grouse habitat [Saskatchewan: Pat Fargey]; ANNOUNCEMENTS: Scientist recognized [Lu Carbyn winner of 2002 William A. Rowan Distinguished Service Award presented by the Alberta Chapter of The Wildlife Society]; Stewardship rewarded [South Okanagan-Similkameen Stewardship Program has won the Excellence in Stewardship category of the 2002 Minister's Environmental Awards in British Columbia]; New Publications; Upcoming event; Site Seeing; FEATURED SPECIES: Reintroducing butterflies - Habitat restoration efforts underway [Ontario: Karner Blue Butterfly, *Lycaeides melissa samuelis*].

Published by the Canadian Wildlife Service, Environment Canada, Ottawa, Ontario K1A 0H3. Edited and designed by West Hawk Associates. Web site: www.cws-scf.ec.gc.ca/es/recovery/archive.html.

TABLE OF CONTENTS *(concluded)*

An *in situ* observation of webover hunting by the Giant Pacific Octopus, *Enteroctopus dofleini* (Wülker, 1910) — James A. Cosgrove — 117

Heavy metal concentrations in Arctic Foxes, *Alopex lagopus*, in the Prudhoe Bay Oil Field, Alaska — Warren B. Ballard, Matthew A. Cronin, Martin D. Robards, and William A. Stubblefield — 119

Winter occurrence of Harlan's, *Buteo jamaicensis harlani*, and Krider's, *B. j. borealis*, hawks in eastern Kansas — Roger C. Applegate and Deborah R. Applegate — 122

Feral dogs, *Canis familiaris*, kill Coyote, *Canis latrans* — Jan F. Kamler, Kurt Keeler, Galen Wiens, Chad Richardson, and Philip S. Gipson — 123

Feature

Vegetation classification standard for Canada Workshop: 31 May - 2 June 2000 — Rob Alvo and Serguei Ponomarenko — 125

Tribute

A tribute to William Earl Godfrey, 1910-2002 — Michel Gosselin, Edward L. Bousfield, and Stewart D. MacDonald — 140

Book Reviews

Zoology: Sibley's Birding Basics — Fishes of Alaska — Evolution, Ecology, Conservation, and Management of Hawaiian Birds: A Vanishing Avifauna — Global Register of Migratory Species (GROMS): Database, GIS Maps, and Threat Analysis — Carnivore Conservation — Knowing Bass: The Scientific Approach to Catching More Fish — Life Underground, the Biology of Subterranean Rodents — Weird Nature: An Astonishing Exploration of Nature's Strangest Behavior — The Birds of Heaven: Travels with Cranes — 151

Botany: A Flora of Glacier National Park, Montana — 159

Environment: Bringing the Biosphere Home, Learning to Perceive Global Environmental Change — Trees, Shrubs, and Vines for Attracting Birds — 159

New Titles — 161

News and Comment

Amphipacifica: Journal of Aquatic Systematic Biology 3(3) — *Froglog*: Newsletter of the Declining Amphibian Populations Task Force (54, 55) — Point Pelee Natural History News 2(4) — Curatorial Reports on Natural History Topics: Nova Scotia Museum of Natural History — Canadian Species at Risk: November 2002 — *Amphibian Voice* Winter 2002 — *Marine Turtle Newsletter* (99) — *Recovery*: An Endangered Species Newsletter (23) — 164

Mailing date of the previous issue 116(4): 16 May 2003

Articles

Birds and mammals of the St. Elias Mountain Parks: Checklist evidence for a biogeographic convergence zone — Ryan K. Danby

Distribution of, and microhabitat use by, woodland salamanders along forest-farmland edges — Gretchen I. Young and Richard H. Yahner

Distribution, abundance, and status of the Greater Sage-Grouse, *Centrocercus urophasianus*, in Canada — Cameron L. Aldridge and R. Mark Brigham

Age structure differences in American Mink, *Mustela vison*, populations under varying harvest regimes — Jackson S. Whitman

On the vertical zonation of hair lichens (*Bryoria*) in the canopies of high-elevation oldgrowth conifer forests — Trevor Goward

On the dispersal of hair lichens (*Bryoria*) in high-elevation oldgrowth conifer forests? — Trevor Goward

Sympatric presence of low and high gillraker forms of Cisco, *Coregonus artedi*, in Lake Athapapuskow, Manitoba — Katherine A. A. Aoki and R. A. Bodaly

Sightings of vagrant Pacific alcids in Desolation Sound, British Columbia — Laura McFarlane Tranquilla, Falk Huettmann, Cecilia Lougheed, Lynn Lougheed, Nadine Parker and Gary Kaiser

Range extensions of Logperch, *Perca caprodes*, and Longnose Dace, *Rhinichthys cataractae*, in Newfoundland and Labrador — Robert Perry and Tammy L. Joyce

Notes on the *Populus* "dipzone effect" on lichens in well-ventilated stands in east-central British Columbia — Trevor Goward and André Arsenault

Eco-geographical and cytological notes on the Entire-leaved Daisy, *Hulteniella intergrifolia* (Asteraceae), in Québec — Norman Dignard and Camille Gervais

Status of the Largest Breeding Concentration of Atlantic Puffins, *Fratercula arctica*, in North America — Michael S. Rodway, Heidi M. Regehr, and John W. Chardine

Response of male Mountain Chickadees (*Poecile gambeli*) to playback of different song types — Myra O. Wiebe and M. Ross Lein

Are there two species of Pygmy Shrews (*Sorex*)? Revisiting the question using DNA sequence data — Donald T. Stewart, Michelle McPherson, Jody Robichaud, and Luca Fumagalli

Reintroducing fire for conservation of fescue prairie association remnants in the northern Great Plains — J. T. Romo

A brief history of Purple Loosestrife, *Lythrum salicaria*, in Manitoba and its status in 2001 — Cory J. Lindgren

Comparison of spring return dates of Mountain Bluebirds, *Sialia currucoides*, and Tree Swallows, *Tachycineta bicolor*, with monthly air temperatures — Robert K. Lane and Myrna Pearman

Notes

Mortality of Black Bears, *Ursus americanus*, associated with elevated train trestles — Kyle R. Van Why and Michael J. Chamberlain

Incidence of Mink, *Mustela vision*, and River Otter, *Lutra canadensis*, in a highly urbanized area — L. David Mech

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 01226 6177

ISSN 0008-3550

QH
1
C213
NH

The CANADIAN FIELD-NATURALIST

Published by THE OTTAWA FIELD-NATURALISTS' CLUB, Ottawa, Canada

Volume 117, Number 2

April–June 2003

The Ottawa Field-Naturalists' Club

FOUNDED IN 1879

Patrons

Her Excellency The Right Honourable Adrienne Clarkson, C.C., C.M.M., C.D.
Governor General of Canada
His Excellency John Ralston Saul, C.C.

The objectives of this Club shall be to promote the appreciation, preservation and conservation of Canada's natural heritage; to encourage investigation and publish the results of research in all fields of natural history and to diffuse information on these fields as widely as possible; to support and cooperate with organizations engaged in preserving, maintaining or restoring environments of high quality for living things.

Honorary Members

Edward L. Bousfield
Donald M. Britton
Irwin M. Brodo
William J. Cody
Francis R. Cook
Ellaine Dickson
Bruce Di Labio
R. Yorke Edwards
Anthony J. Erskine
John M. Gillett
C. Stuart Houston
George F. . Ledingham
John A. Livingston
Stewart D. MacDonald
Hue N. MacKenzie
Theodore Mosquin
Eugene G. Munroe
Robert W. Nero
E. Franklin Pope
William O. Pruitt,, Jr.
Joyce and Allan Reddoch
Mary E. Stuart
John B. Theberge
Sheila Thomson

2003 Council

President: Gary McNulty
Vice-President: Mike Murphy
Gillian Marston
Recording Secretary: Ken Alhson
Treasurer: Frank Pope
Past President: Eleanor Zurbrigg
Ronald E. Bedford
John Cameron
Janet Castle
Charlie Clifford
William J. Cody
Kathy Conlan
Francis R. Cook
Barbara Gaertner
Marcel Gahbauer
Diane Lepage
Karen McLachalan Hamilton
David Hobden
Cendrine Huemer
John Roy
Stanley Rosenbaum
Louise Schwartz
David Smythe
Chris Traynor

To communicate with the Club, address postal correspondence to: The Ottawa Field-Naturalists' Club, P.O. Box 35069, Westgate P.O. Ottawa, Canada K1Z 1A2, or e-mail: ofnc@achilles.net.
For information on Club activities telephone (613) 722-3050 or check http//www.achilles.net/ofnc/index.htm

The Canadian Field-Naturalist

The *Canadian Field-Naturalist* is published quarterly by The Ottawa Field-Naturalists' Club. Opinions and ideas expressed in this journal do not necessarily reflect those of The Ottawa Field-Naturalists' Club or any other agency.

We acknowledge the financial support of the Government of Canada toward our mailing cost through the Publication Assistance Program (PAP), Heritage number 09477.

Editor: Dr. Francis R. Cook, R.R. 3, North Augusta, Ontario KOG IR0; (613) 269-3211; e-mail: fcook@achilles.net
Copy Editor: Elizabeth Morton
Business Manager: William J. Cody, P.O. Box 35069, Westgate P.O. Ottawa, Canada KIZ 1A2 (613) 759-1374
Book Review Editor: Dr. J. Wilson Eedy (deceased 23 June 2003);
Roy John (appointed August 2003), 2193 Emard Crescent, Ottawa, Ontario K1J 6K5
email: roy.john@pwgsc.gc.ca

Associate Editors:
Robert R. Anderson
Charles D. Bird
Robert R. Campbell
Paul M. Catling
Brian W. Coad
Anthony J. Erskine
David Nagorsen
Donald F. McAlpine
William O. Pruitt, Jr.

Chairman, Publications Committee: Ronald E. Bedford

All manuscripts intended for publication should be addressed to the Editor and sent by postal mail. Book-review correspondence should be addressed to Roy John, Book-review Editor.

Subscriptions and Membership
Subscription rates for individuals are $28 per calendar year. Libraries and other institutions may subscribe at the rate of $45 per year (volume). The Ottawa Field-Naturalists' Club annual membership fee of $28 (individual) $30 (family) $50 (sustaining) and $500 (life) includes a subscription to *The Canadian Field-Naturalist*. All foreign subscribers and members (including USA) must add an additional $5.00 to cover postage. The club regional journal, *Trail & Landscape*, covers the Ottawa District and Local Club events. It is mailed to Ottawa area members, and available to those outside Ottawa on request. It is available to Libraries at $28 per year. Subscriptions, applications for membership, notices of changes of address, and undeliverable copies should be mailed to: The Ottawa Field-Naturalists Club, P.O. Box 35069, Westgate P.O. Ottawa, Canada K1Z 1A2. Canada Post Publications Mail Agreement number 40012317. Return Postage Guaranteed. Date of this issue: April–June 2003. (February 2004).

COVER: Coastal fringe forest on a steep slope above Burnett Beach, British Columbia central coast. Photograph by Eric Lamb. See article pages 209-217.

SMITHSONIAN
MAR 15 2004
LIBRARIES

The Canadian Field-Naturalist

Volume 117, Number 2 April–June 2003

Effects of Plant Cover Improvements for Nesting Ducks on Grassland Songbirds

Stéphane Lapointe[1], Luc Bélanger[2], Jean-François Giroux[1,4], . Bernard Filion[3]

[1] Université du Québec à Montréal, Département des sciences biologiques, Box 8888, Station Centre-Ville, Montréal, Québec H3C 3P8 Canada; corresponding author.
[2] Environment Canada, Canadian Wildlife Service, 1141 Route de l'Église, Box 10100, Ste. Foy, Québec G1V 4H5 Canada
[3] Ducks Unlimited Canada, 710 Bouvier St., Suite 260, Québec, Québec G2J 1A7 Canada
[4] Corresponding author Giroux.Jean-François@UQAM.ca

Lapointe, Stéphane, Luc Bélanger, Jean-François Giroux, and Bernard Filion. 2003. Effects of plant cover improvements for nesting ducks on grassland songbirds. Canadian Field-Naturalist 117(2): 167-172.

Several islands located along the St. Lawrence River in southern Quebec have been used as natural pastureland by cattle for decades. Recently, a rest-rotation grazing system and dense nesting cover were established on four islands near Varennes to improve duck nesting conditions. The effects of these two plant cover improvements on the abundance of grassland songbirds were assessed through four treatments: (1) idle fields with no vegetation improvement but exclusion of cattle (IDLE), (2) improved pastures with seeding of forage plants for cattle (IMPP), (3) dense seeded nesting cover fields improved for ducks and where cattle were excluded (DNC), and (4) natural or unimproved pastures grazed by cattle after the duck nesting season (UIPP). The overall abundance of birds was similar among treatments before cover improvements as well as two years after. The abundance of Bobolinks (*Dolichonyx oryzivorus*) was significantly greater in DNC and UIPP two years after treatments while Red-winged Blackbirds (*Agelaius phoeniceus*) were more abundant in DNC and IDLE. Plant cover improvements had little impact on Savannah Sparrow (*Passerculus sandwichensis*) abundance. Furthermore, few annual or treatment-related changes were observed for less abundant species. On the short-term, duck nesting cover improvements in natural pastures did not have any major effect on grassland songbirds on Varennes islands.

Key Words: ducks, nesting, plant cover, grassland, songbirds, Québec.

Since the early 1950s, intensive farming practices have radically transformed the agricultural landscape of North America, which resulted in many negative effects on ground-nesting grassland birds (Sugden and Beyersbergen 1984; Best et al. 1990; Askins 1993). Cattle grazing, for example, has greatly expanded in most regions, and improvements in forage crops and range management have allowed farmers to increase stocking rates (Barker et al. 1990). By modifying the quality of plant cover (Kantrud and Kologiski 1982; Fleischner 1994), cattle reduce both the diversity of birds and their breeding densities (Bowen and Kruse 1993; Bélanger and Picard 1999). Grazing also reduces the quantity of residual vegetation available for nest construction and as substratum for invertebrate prey species, which in turn, may affect bird breeding and/or foraging (Heitchmidt et al. 1982; Quinn and Walgenbach 1990). Nesting cover modified by trampling can also increase predation and parasitism (Jensen et al. 1990; Johnson and Temple 1990).

It has been shown that proper habitat management such as rotational grazing systems and the establishment of dense-seeded nesting cover can greatly improve nesting conditions for waterfowl (Gjersing 1975; Klett et al. 1988; Barker et al. 1990; Lokemoen et al. 1990; Lapointe et al. 2000). However, the effect of such techniques on other grassland ground-nesting bird species is poorly understood (Johnson et al. 1994).

In Québec, close to 40% of the 5000 ha of islands of the St. Lawrence River has been used for decades as natural pastureland (Bélanger and Lehoux 1995), thereby compromising the value of these islands as duck-nesting habitat (Bélanger and Picard 1999). Consequently, a project to improve waterfowl nesting and brood-rearing habitat, as well as to limit riverbank erosion and overgrazing problems, was initiated in 1992 on the Varennes islands by establishing a rest-rotation grazing system and plots of dense nesting cover. In a previous paper, Lapointe et al. (2000) reported the benefits of these plant cover improvements to island-

nesting ducks. The objective of this study was to assess the short-term effects of plant cover improvements on the abundance of ground-nesting grassland songbirds.

Study Area

The 115-ha Varennes archipelago (45° 40' N, 73° 27' W) is located 20 km northeast of Montreal (Canada) along the St. Lawrence River. It is composed of four islands ranging in size from 9.4 to 59.8 ha (Figure 1). Before cover improvements, the dominant plant species on these islands were Tufted Vetch (*Vicia cracca*), Redtop (*Agrostis alba*), Red Fescue (*Festuca rubra*) and Kentucky Bluegrass (*Poa pratensis*). On one island (Grande-île), however, tall grasses such as *Phalaris arundinacea* and *Calamagrostis canadensis* were dominant. As a result of continuous grazing pressure, trees and shrubs are absent. Emergent marsh vegetation consists primarily of cattails (*Typha angustifolia*) and scattered clumps of Giant Bur-reed (*Sparganium eurycarpum*) and arrowheads (*Sagittaria* spp.).

Communal pasture is a traditional agricultural practice on islands of the freshwater section of the St. Lawrence River in Québec (Bélanger and Picard 1999). Approximately 100 cows are present each year on the Varennes islands from late May-early June to mid-November. Before 1993, cows roamed freely over the four islands. In fall 1992, Ducks Unlimited Canada initiated a controlled grazing system; one 19-ha pasture was seeded with a mixture of Timothy (*Phleum pratense*), Yellow Sweet-Clover (*Melilotus officinalis*), Smooth Brome (*Bromus inermis*) and clovers (*Trifolium* spp.) to improve the quality of the forage (improved pasture – IMPP). A dense nesting cover (DNC93) was also established on a 5-ha plot by seeding Reed Canary Grass (*Phalaris arundinacea*). The remaining parts of the islands were left in their natural state with some being grazed by cattle after the duck-nesting season (27.4 ha of unimproved pastures – UIPP) or left undisturbed by excluding cattle (59.9 ha of idle fields – IDLE). All seeded fields were previously treated with herbicide and ploughed. In summer 1993, the rest-rotational grazing system limited cattle to approximately 50% of the islands, in rotation between IMPP and UIPP. In fall 1993, the treatments were completed with the seeding of two additional plots of dense nesting cover (15.0 ha of DNC – DNC94) with a mixture of Western Wheatgrass (*Agropyron smithii*) and Crested Wheatgrass (*A. cristatum*). Finally, a 17.6-ha portion of old pasture had been ploughed for future works (PLGH). More details may be found in Lapointe et al (2000).

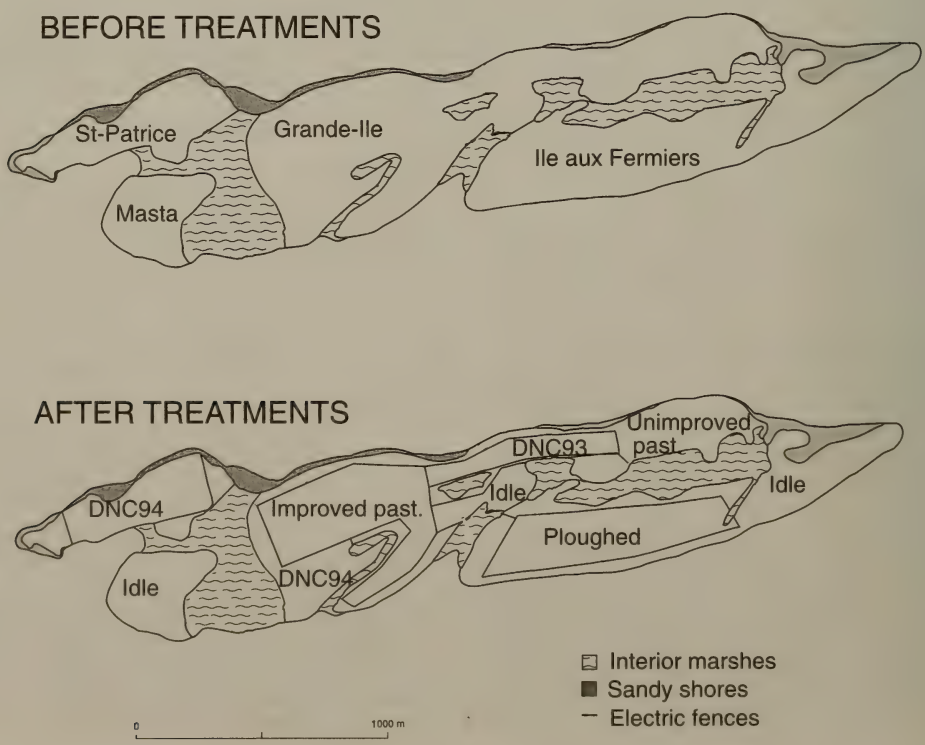


FIGURE 1. The four islands of Varennes archipelago along the St. Lawrence River (Quebec) before (1992) and after (1993-1994) plant cover improvements for nesting ducks.

Material and Methods

Experimental design and bird surveys

Because it was impossible to find other islands similar in size, plant cover types, spring flooding conditions, past and present grazing intensity, we did not attempt to set up a large scale spatially replicated experiment. Instead, we tried to circumvent the problem with a temporal control by taking comparative measures of plant cover use by birds within the same sampling plots before and after cover improvements (see Lapointe et al. 2000).

Birds were surveyed in 50 0.5 ha-plots (50 × 100 m) distributed randomly over the upland portions of the islands. The four corners of each plot were marked with posts and the same plots were surveyed from 1992 to 1994. However, treatments to which these plots belonged varied from year to year in relation to habitat modifications. An observer located in the centre of the plot recorded all the birds heard and seen during a 5-min period after a 2-min delay before the count began. Birds flying over the plots were not counted. Surveys were done during five consecutive days in early June, between 05:00 and 10:00, whenever weather conditions were adequate.

Data analyses

For each species, we totalled the number of males and females recorded in each plot for a given date. We first conducted a series of ANOVA for each year and species to compare the relative abundance of individuals among survey dates. For each species, we then used the day with the maximum number of birds recorded and compared their relative abundance among treatments and years with ANOVA. Maxima were used because detection probability of individuals is always <1 during such surveys. Logarithmic transformations were used because the data were not normally distributed and the variances were not homogeneous. Differences among treatments and years were determined using multiple comparison tests (LSD). Finally, the species composition (proportion of individuals of each species) was compared among years using χ^2 tests. Means are presented ± 1 SE throughout the text and tables.

Results

Species composition and bird abundance

Totals of 1638, 1738, and 1507 bird observations were recorded in 1992, 1993, and 1994, respectively. Each year, the mean number of birds/plot did not differ among the five survey dates for all species except two. The number of Savannah Sparrows (*Passerculus sandwichensis*) was always higher towards the end of the sampling period indicating that some birds arrived on the breeding grounds during the survey period (1992: $F_{4,244} = 15.4$, $P = 0.0001$; 1993: $F_{4,245} = 2.5$, $P = 0.04$; 1994: $F_{7,384} = 11.7$, $P = 0.0001$). On the other hand, the number of Song Sparrows (*Melospiza melodia*) was three times larger during the first day of the survey in 1992 than later indicating that migrating birds were still passing through the area ($F_{4,244} = 12.7$, $P = 0.0001$). This count was therefore discarded and we used the second highest count for the analyses.

Although 15 species were observed on the islands, Savannah Sparrows, Bobolinks (*Dolichonyx oryzivorus*) and Red-winged Blackbirds (*Agelaius phoeniceus*) represented 92% of the observations. The relative abundance of these species varied among years (χ^2 = 68.5; df = 8; P<0.001). Savannah Sparrows were more abundant in 1993 than in 1992 and 1994, and the opposite was true for Red-winged Blackbirds. Bobolinks were less abundant in 1993 and 1994 than in 1992. Other species occurred at low densities and included Common Snipe (*Gallinago gallinago*), Swamp Sparrow, Wilson's Phalarope (*Phalaropus tricolor*), Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni*), Marsh Wren (*Cistothorus palustris*), Chipping Sparrow (*Spizella passerina*), Eastern Kingbird (*Tyrannus tyrannus*), Horned Lark, Lincoln Sparrow (*Melospisa linconii*) and Eastern Meadowlark (*Sturnella magna*).

Effects of cover improvements

Before habitat improvements (1992), the mean number of birds was similar among future treatment areas ($F_{3,46} = 1.55$, $P = 0.22$; Table 1). After the rest-rotation grazing system had been implemented and dense cover sown (1993), the greatest number of birds was found in IDLE ($F_{3,46} = 6.06$, $P = 0.002$). In 1994, the mean number of birds was similar in all treatments except in PLGH where fewer individuals were recorded ($F_{3,48} = 4.29$, $P = 0.003$).

The mean number of birds in IDLE increased in 1993, but returned to an intermediate level in 1994 ($F_{2,56} = 3.33$, $P = 0.04$; Table 1). In IMPP, the number of birds decreased after controlling cattle movement ($F_{2,33} = 4.81$, $P = 0.01$). Bird abundance also decreased in UIPP after the first year but increased in 1994 ($F_{2,21} = 3.95$, $P = 0.03$). Bird numbers in DNC93 remained constant over years ($F_{2,12} = 0.88$, $P = 0.44$).

We further investigated the effect of habitat improvements by looking at the annual abundance of individual species. In 1992, the average number of Savannah Sparrows was similar in all future treatments ($F_{3,46} = 0.32$, $P = 0.81$; Table 2). In 1993, they were more common in IDLE and IMPP than in the newly seeded DNC93 ($F_{3,46} = 5.96$, $P = 0.002$) and less in 1994 ($F_{5,43} = 4.68$, $P = 0.002$). Bobolink numbers were similar in all treatments, both before and after the first year following cover improvements (1992: $F_{3,46} = 0.32$, $P = 0.18$; 1993: $F_{3,46} = 0.44$, $P = 0.73$; Table 2). Differences appeared in 1994 when a greater number of bobolinks was recorded in the two-year-old DNC93 and UIPP ($F_{5,43} = 3.48$, $P = 0.01$). Unlike the previous species, Red-winged Blackbirds showed significant differences in 1992 among future treatments. They were more abundant in UIPP than in the other treatments and

TABLE 1. Mean (±SE) number of birds/0.5-ha plot for all species of birds in six treatments on the Varennes islands in 1992 (pre-treatment year) and 1993-1994 (post-treatment years).

Treatment	n[1]	1992	1993	1994
IDLE	23, 23, 13	7.3±0.9 a,A[2]	10.0±0.6 a,B	8.5±1.0 ab,AB
IMPP	12, 12, 12	10.3±1.2 a,A	7.1±1.1 b,B	6.0±0.7 ab,B
UIPP	10, 10, 4	9.2±1.2 a,AB	5.8±0.7 b,B	11.3±3.0 a,A
DNC93[3]	5, 5, 5	9.2±1.2 a,A	8.2±0.9 ab,A	11.4±2.7 a,A
DNC94[4]	1, 1, 7	–	–	7.0±1.1 ab
PLGH	1, 1, 8	–	–	4.1±0.8 b

[1] Number of plots surveyed in 1992, 1993, and 1994, respectively.
[2] Lower case letters indicate significant differences among treatments for a given year while upper case letters indicate significant differences among years for a given treatment (LSD, $P<0.5$).
[3] DNC seeded in 1992 and first available in 1993.
[4] DNC seeded in 1993 and first available in 1994.

more abundant in IMPP than in DNC93 ($F_{3,46}$ = 12.02, P = 0.0001; Table 2). In 1993, Red-winged Blackbird numbers were similar in all treatments ($F_{3,46}$ = 0.81, P = 0.49) while they increased in IDLE, UIPP and the two-year-old DNC93 in 1994 ($F_{5,43}$ = 8.22, P = 0.0001).

Few annual or treatment-related changes were observed for the less abundant species. Song Sparrows were found in all treatments while Common Snipes were found in UIPP each year and in PLGH and IMPP in 1994. Wilson's Phalaropes were observed in UIPP during all years and in IDLE in 1992 and 1993. Swamp Sparrows were recorded in UIPP (1993 and 1994), IDLE, and DNC93. Uncommon species like the Nelson's Sharp-tailed Sparrow and Marsh Wren were seen in different treatments, but did not seem to favour one over the others during the three years of the study.

Discussion

Integrating traditional agricultural practices and wildlife needs has been a major component of the conservation plan proposed for the St. Lawrence River islands (see Bélanger and Lehoux 1995). Stocking rate >1 cow/ha/yr can reduce bird diversity and breeding densities by modifying cover quality (Bélanger and Picard 1999). Consequently, grazing management has been implemented to improve plant cover conditions, especially for nesting ducks (Lapointe et al. 2000). However, the effects of such techniques on other grassland birds have remained poorly understood (Johnson et al. 1994).

Before cover improvements, grazing had a significant impact on plant cover on the Varennes islands by reducing green vegetation biomass by more than 50% in a single season (Lapointe et al. 2000). All the islands were grazed uniformly resulting in a similar cover quality among treatments before the experimental work. The introduction of a rest-rotation grazing system helped to lessen the impact of cattle on the vegetation and allowed the establishment of a high-quality nesting cover for ducks (Lapointe et al. 2000). Two years after cover improvements, more litter was found in DNC and IDLE and greater levels of visual obstruction were noted in DNC. Our study shows that these changes had little effects on the overall abundance of grassland birds. All treatments were located in open habitats and the well-delimited plots were easily surveyed in all treatments. We therefore believe that no observability bias existed among treatments before or after the management works.

Community analysis may sometimes conceal different levels of tolerance among individual species (Bock et al. 1993). We therefore tested for changes in numbers for the three most abundant species. Cover improvements seemed to have little impact on Savannah Sparrow abundance. This species generally favours idle fields with tall vegetation (Owens and Myres 1973; Kantrud 1981) but was equally attracted to IDLE, DNC, IMPP, and UIPP on the Varennes islands. Numbers also remained unchanged in IMPP when the intensity of grazing increased. Savannah Sparrow generally does not tolerate intensive grazing (Bock et al. 1993). However, since this species begins nesting in mid-May in our area (Gauthier and Aubry 1996), it may be more tolerant to cattle grazing, which began in late May-early June at Varennes. Although no effects of cover improvements were observed for Bobolinks in the first year they subsequently were more abundant in DNC and UIPP. This could be related to their preference for nesting in tall vegetation with a dense litter (Kantrud 1981; Bollinger and Gavin 1992). The greater number of Red-winged Blackbirds in UIPP before cover improvements cannot be explained by differences in plant cover quality as it was similar among treatments (Lapointe et al. 2000). However, two years after, redwings preferred treatments with greater amounts of residual vegetation and better levels of visual obstruction (IDLE and DNC), which support observations by Searcy (1979).

It was more difficult to assess the impact of cover improvement on less common species because of their low abundance. We found several nests of Wilson's

TABLE 2. Mean number (± SE) of Savannah Sparrows, Bobolinks, and Red-winged Blackbirds/0.5-ha plot in six treatments on the Varennes islands in 1992 (pre-treatment year) and 1993-1994 (post-treatment years). Numbers of plots surveyed are given in Table 1.

Treatment	Savannah Sparrow			Bobolink			Red-winged Blackbird		
	1992	1993	1994	1992	1993	1994	1992	1993	1994
IDLE	3.9±0.6 a,B[1]	6.9±0.6 a,A	2.9±0.4 cd,B	1.7±0.3 a,A	1.3±0.3 a,A	1.2±0.4 bc,A	0.9±0.2 bc,B	1.6±0.5 a,B	3.6±0.5 a,A
IMPP	4.5±0.8 a,A	4.8±0.8 ab,A	4.3±0.4 abc,A	2.6±0.7 a,A	1.6±0.4 a,A	0.8±0.3 c,A	2.1±0.6 b,A	0.9±0.3 a,B	0.5±0.2 b,B
UIPP	3.4±0.7 a,A	4.2±0.7 bc,A	4.5±0.7 ab,A	2.0±0.4 a,A	1.0±0.3 a,A	2.5±0.9 a,A	3.9±0.5 a,A	0.9±0.2 a,B	4.5±0.7 a,A
DNC93[2]	4.2±0.6 a,AB	2.2±0.9 c,B	5.2±0.9 a,A	3.4±0.8 a,A	1.0±0.6 a,B	2.4±0.4 ab,AB	0.4±0.2 c,B	0.6±0.6 a,B	4.6±1.8 a,A
DNC94[3]	–	–	3.1±0.3 bcd	–	–	0.7±0.6 c	–	–	1.3±0.5 b
PLGH	–	–	2.5±0.3 d	–	–	0.1±0.1 c	–	–	1.0±0.4 b

[1] Lower case letters indicate significant differences among treatments for a given year while upper case letters indicate significant differences among years for a given treatment (LSD, $P<0.05$).
[2] DNC seeded in 1992 and first available in 1993.
[3] DNC seeded in 1993 and first available in 1994.

Phalarope, a species that has recently expanded into the east (Gauthier and Aubry 1996). Nelson's Sharp-tailed Sparrow, a rare species usually found in *Spartina* tidal marshes of the St. Lawrence estuary, was also recorded several times on the islands. The distribution of those species did not change significantly after cover improvements and it seems to be linked to other habitat features. Many of these species use wetlands and riparian areas of the archipelago, and this may be more important than the treatments *per se*.

In conclusion, our study showed that cover improvements for nesting ducks in natural pastures did not have any major effects on the abundance of other ground-nesting species. The nesting cover improvements carried out on the Varennes islands were relatively recent, and only their short-term effects (two years) have been evaluated. As time goes on, IDLE will revert to oldfields (presence of shrubs), and DNC will be better established (more litter). We think that the resulting enhanced habitat quality will be more tangible then, resulting in an increase in songbird abundance.

Acknowledgments

We thank C. Berthiaume, F. Blouin, A. Cossette, G. Couture, A. Girard, S. Goupil, J. Hamel, and C. Miqueu for conducting bird surveys. We would also like to thank the staff of Ducks Unlimited Canada (Québec field office) for carrying out nesting cover improvement and for providing information on grazing regime, and the establishment of duck nesting cover. This project was funded by the Canadian Wildlife Service of Environment Canada under the Eastern Habitat Joint Venture. We are also grateful to D. Lehoux (Canadian Wildlife Service, Québec region) for his contribution at the beginning of the study. Financial and logistic support was also provided by the Université du Québec à Montréal. Finally, we thank P. Drapeau, J. B. Pollard, and J-P Savard for their critical comments on a previous version of this manuscript.

Literature Cited

Askins, R. A. 1993. Populations trends in grassland, shrubland and forest birds in eastern North America. Current Ornithology 11: 1-34.

Barker, W. T., K. K. Sedivec, T. A. Messmer, K. F. Higgins, and **D. R. Hertel.** 1990. Effects of specialized grazing sytems on waterfowl production in southcentral North Dakota. Transactions of North American Wildlife and Natural Resources Conference 55: 462-474.

Basore, N. S., L. B. Best, and **J. B. Wooley.** 1986. Bird nesting in Iowa no-tillage and tilled cropland. Journal of Wildlife Management 50: 19-28.

Bélanger, L., and **D. Lehoux.** 1995. Use of various habitat types by nesting ducks on islands in the St. Lawrence River between Montréal and Trois-Rivières. Environment Canada, Canadian Wildlife Service, Occasional paper number 87. 27 pages.

Bélanger, L., and **M. Picard.** 1999. Cattle grazing and avian communities of the St. Lawrence River islands. Journal of Range Management 52: 332-338.

Bellrose, F. C., and **J. B. Low.** 1978. Advances in waterfowl management research. Wildlife Society Bulletin 6: 63-72.

Best, L. B., R. C. Whitmore, and **G. M. Booth.** 1990. Use of cornfields by birds during the breeding season: the importance of edge habitat. American Midland Naturalist 123: 84-99.

Bock, C. E., V. A. Saab, T. D. Rich, and **D. S. Dobkin.** 1993. Effects of livestock grazing on neotropical migratory landbirds in western North America. Pages 296-309 *in* Status and Management of Neotropical Migratory Birds. *Edited by* D. M. Finch and P. W. Stangel. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. General Technical Report RM-229. Fort Collins, Colorado.

Bollinger, E. K., and **T. A. Gavin.** 1992. Eastern Bobolinks populations: ecology and conservation in an agricultural landscape. Pages 497-506 *in* Ecology and conservation of neotropical migrant landbirds. *Edited by* J. M. Hagan and D. W. Johnston. Smithsonian Institution Press, Washington, D.C.

Bowen, B. S., and **A. D. Kruse.** 1993. Effects of grazing on nesting by upland sandpipers in Southcentral Dakota. Journal of Wildlife Management 57: 291-301.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in Western America. Conservation Biology 8: 629-644.

Gauthier, J., and **Y. Aubry.** *Editors.* 1996. The breeding birds of Québec: atlas of the breeding birds of southern Québec. Association Québécoise des groupes ornithologiques, Province of Québec Society for the Protection of Birds, Canadian Wildlife Service, Environment Canada (Québec region). Montréal. 1295 pages.

Gjersing, F. M. 1975. Waterfowl production in relation to rest-rotation grazing. Journal of Range Management 28: 37-42.

Heitschmidt, R. K., D. L. Price, R. A. Gordon, and **J. R. Frasure.** 1982. Short duration grazing at the Texas Experimental Ranch: effects on aboveground net primary production and seasonal growth dynamics. Journal of Range Management 35: 367-371.

Jensen, H. P., D. Rollins, and **R. L. Gillen.** 1990. Effects of cattle stock density on trampling loss of simulated ground nests. Wildlife Society Bulletin 18: 71-74.

Johnson, R. G., and **S. A. Temple.** 1990. Nest predation and brood parasitism of tallgrass prairie birds. Journal of Wildlife Management 54: 106-111.

Johnson, D. H., R. L. Kreil, G. B. Berkey, R. D. Crawford, D. O. Lambeth, and **S. F. Galipeau.** 1994. Influences of waterfowl management on nongame birds: the North Dakota experience. Transactions of North American Wildlife and Natural Resources Conference 59: 293-302.

Kantrud, H. A. 1981. Grazing intensity effects on the breeding avifauna of North Dakota native grasslands. Canadian Field-Naturalist 95: 404-417.

Kantrud, K. H., and **R. L. Kologiski.** 1982. Effects of soils and grazing on breeding birds of uncultivated upland grasslands of the Northern Great Plains. U. S. Department of the Interior. U. S. Fish and Wildlife Service. Report 15. 33 pages.

Klett, A. T., T. L. Shaffer, and **D. H. Johnson.** 1988. Duck nest success in the Prairie pothole region. Journal of Wildlife Management 52: 431-440.

Lapointe, S., J.-F. Giroux, L. Bélanger, and **B. Filion.** 2000. Benefits of rotational grazing and dense nesting cover for island-nesting waterfowl in southern Québec. Agriculture, Ecosystems and Environment 78: 261-272.

Lokemoen, J. T., H. F. Duebbert, and **D. E. Sharp.** 1990. Homing and reproductive habits of mallards, gadwalls, and blue-winged teal. Wildlife Monographs 106: 1-28.

Owens, R. A., and **M. T. Myres.** 1973. Effects of agriculture upon populations of native passerine birds of an Alberta fescue grassland. Canadian Journal of Zoology 57: 697-713.

Quinn, M. A., and **D. D. Walgenbach.** 1990. Influence of grazing history on the community structure of grasshoppers of a mixed-grass prairie. Environmental Entomology 19: 1756-1766.

Searcy, W. A. 1979. Female choice of mates: a general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). American Naturalist 114: 77-100.

Sugden, L. G., and **G. W. Beyersbergen.** 1984. Farming intensity on waterfowl breeding grounds in Saskatchewan parklands. Wildlife Society Bulletin 12: 22-26.

Received 20 December 2000
Accepted 28 July 2003

Winter Bird Use of Urban and Rural Habitats in Ontario

Paul G. R. Smith

Resource Management Branch, Ministry of Agriculture and Food, 1 Stone Road West, 3rd Floor South, Guelph, Ontario N1G 4Y2 Canada

Smith, Paul G. R. 2003. Winter bird use of urban and rural habitats in Ontario. Canadian Field-Naturalist 117(2): 173-183.

This study examined variation in winter bird diversity, abundance, biomass and species and guild composition on plots in farmland, rural forests, mixed rural habitat, cities and three categories of urban natural areas in southern Ontario. Small (<20 g), insectivorous, upper canopy, bark foraging and forest species were more prevalent in rural mixed habitat, urban natural areas and especially rural forests. Larger (20-100 g), ground feeding and omnivorous birds typified cities and farms. Many bird species classified as forest, forest edge and field species during summer also favored these same habitats during winter. The 52 sample plots can be accurately classified into the seven habitat categories through discriminant analysis using the percentages of small species, insectivores, forest species and alien species. Urban natural areas, forests and mixed rural habitat showed the highest diversity while cities and farms showed the lowest diversity. Both bird abundance and biomass were highest in urban natural areas with open water and urban residential and commercial areas, whereas both were lowest in farmland.

Key Words: bird populations, urban ecology, winter, urban-rural ecological gradient, Ontario.

The landscapes of Ontario south of the Canadian Shield, like much of eastern North America, are mosaics of cities, farms, forests and successional habitats. The effects of urbanization, farming and fragmentation on breeding birds have been widely studied. This is less true of wintering birds (Erskine 1980; 1992; Hohtola 1978; Lancaster and Rees 1979; Blake 1987; Tilghman 1987; Telleria and Santos 1995; Morneau et al. 1996). Understanding the effects of landscape change on birds depends on knowledge of effects of habitat on birds during all seasons. This paper compares and contrasts winter bird use of seven urban and rural habitat categories in terms of avian diversity, abundance, biomass, bird size, guilds and species composition.

Urban ecosystems generally have lower biological diversity compared to forests and rural habitats (Gilbert 1989; Adams 1994; Marzluff et al. 1998). However, along with the lower diversity, urban bird assemblages often show greater abundance and biomass than do those in forests (Erskine 1980; Hohtola 1978; Lancaster and Rees 1979; Adams 1994).

Farmland is a mosaic of habitats for birds, but many farmland birds are edge species associated with hedgerows and remnant natural vegetation, and other typically urban species may be associated with farm buildings (Rodenhouse et al. 1995). Relatively few species are specifically associated with croplands (Møller 1984). Nevertheless, some croplands provide considerable food in soil invertebrates and seed (Lack 1992). Areas with more diversity in farm habitats and in farming practices show far greater diversity of bird life (Parrish et al. 1994; Bignal and McCraken 1996; Newton 1998).

The effect on bird life of habitat fragmentation from farming and urbanization is now a central issue in conservation biology (Whitcomb et al. 1981; Ambuel and Temple 1983; Robbins et al. 1989; Saunders et al. 1991; Hinsley et al. 1996; Nour et al. 1999). The affinities of breeding species for field, forest edge and forest habitats are now well established. A few studies suggest that similar affinities exist for wintering bird species (Blake 1987; Tilghman 1987; Telleria and Santos 1995).

Winter and breeding bird assemblages differ in many respects. In temperate regions, bird species-richness and abundance are lower during winter, due to the absence of neotropical and short-distance migrants (Morrison et al. 1987). Snow cover and depth limit ground foraging (Erskine 1980). Winter is a critical time for many resident species, and winter events can affect population levels during the breeding season (e.g., Mehlman 1997). Patterns of species presence have changed not only due to habitat modifications, but also due to increases in bird feeders in urban and rural areas (Root 1988; Wilson 1994).

Periodic "eruptions" of northern seed-eating and raptorial species in particular years during winter can dramatically increase local densities of birds and change species composition (Bock and Lepthien 1976; Root 1988; Hochachka et al. 1999). Intra-species and inter-species flocking is important in winter bird assemblages. This phenomenon relates to the reduced sedentary and territorial behavior during winter and is thought to have adaptive significance (e.g., Berner and Grubb 1985; Morrison et al. 1987).

While many aspects of breeding bird use of different urban and rural habitat categories have been thoroughly studied, research on winter birds is sketchy. Therefore, this research addressed the following specific questions. Are the well-documented differences in diversity, abundance, biomass and species composition among rural and urban breeding bird communities similar for

wintering birds in southern Ontario? How does the more limited range of food types during winter affect the guilds and sizes of birds using different habitat categories? Are the now familiar preferences of breeding bird species for forest, forest edge and field evident in winter habitat use? To address these questions, this study analyzed differences in winter bird use of different habitat categories in rural and urban areas in southern Ontario, Canada. It examined variation in winter bird diversity, abundance, biomass and species and guild composition on plots in farmland, forests, mixed rural habitat, cities and three categories of urban natural areas.

Methods

Study Plots

The Winter Bird Population Study (WBPS) is a method for sampling the winter birds of defined census plots (Kolb 1965; Robbins 1972, 1981). Eight to ten, and occasionally fewer, counts on each fixed-area plot are conducted in December through February. The WBPS method can be robust to the use of different observers on different plots (Smith 1984a).

Fifty-two plots from across southern Ontario were used in this study (Appendix), drawn from those published in *American Birds* and *Ontario Field Biologist*. Further description of some plots can be found elsewhere (Campbell and Dagg 1976; Erskine 1975; Smith et al. 1981, 1982; Smith 1984a, b). Climate varies across the geographic range of locations of these study plots and influences the distribution and abundance of a number of species (Erskine 1980). Climate and other factors contribute to the large year-to-year variation in the winter occurrence and abundance of many species (Bock and Lepthien 1976; Bock and Root 1981; Root 1988; Smith 1984a).

Habitat Classification

The study plots reflect different habitat categories in urban and rural southern Ontario and were classified into seven categories—three rural and urban categories (cf., Brady et al. 1979). These reflect gradients of human modification through urbanization and agriculture. Table 1 summarizes the classification of habitat categories. This classification has significant limitations but provides a basis for assessing some broad scale patterns.

Fourteen of the plots are drawn from a range of rural landscapes including rural forest, mixed rural habitats and farmland.

Seven rural forested plots included deciduous, mixed and coniferous forests (1-7, in Appendix). Six of the plots were within larger continuous protected habitats including conservation lands, Rondeau Provincial Park and St. Lawrence Islands National Park.

Four plots were composed of mixed rural habitats including forest, old field (successional), and agricultural field (8-11, in Appendix).

Three plots composed of farmland were included (50-52 in the Appendix).

Thirty-three plots reflect a range of urban habitat categories including urban and suburban residential, commercial and urban natural areas including parks, urban open space, woodlands and other natural or semi-natural areas within cities and towns. These plots reflect different levels of disturbance along an urbanization gradient.

Twenty-seven plots of urban natural areas included ravines, valleys, woodlots, and parks. Urban natural areas were divided into three categories as described in Table 1. Five plots in urban natural areas with more than 50 m^2 open water during the winter were classified as a separate category, urban natural with water (12-16 in Appendix). The presence of open water is known to significantly influence abundance, diversity and species composition of winter bird assemblages (Tilghman 1987; Gilbert 1989; Adams 1994). The other 22 plots in urban natural areas were divided into those more or less than 10 ha in area (Table 1). Twelve plots were > 10 ha (17-28 in Appendix), while a further ten were < 10 ha (29-38 in Appendix). This division reflects the fact that area is known to significantly influence the diversity and species composition of winter bird assemblages (Blake 1987; Tilghman 1987; Telleria and Santos 1995). Exploratory data analysis of these 27 plots indicated that area and presence of open water were important variables in explaining variance among the 27 plots and therefore a useful means to categorize the urban natural areas.

Urban areas or "cities" included two downtown plots, four plots in older, high-density residential parts of three cities, and one plot in a small town (39-49 in the Appendix). Four other plots were located in suburban, lower-density portions of two cities.

Variables Selected for Analysis

A variety of measures of avian community structure and composition were used to examine variation across the habitat categories. Winter bird diversity, abundance, biomass, mass, guild structure and species composition were all examined.

Ecological and avian diversity have been measured in a wide variety of ways to address different definitions of diversity and methodological issues (Magurran 1988). Consequently, several indices of diversity were employed in this study. The number of species recorded was the measure of species richness. Species richness is known to have inherent and sampling-based biases (Hill 1973; James and Rathbun 1982; Magurran 1988) and so other indices of diversity were used. Simpson's diversity index, N_2 ($N_2=1/\Sigma\ p_i$, where p_i is the proportion of each species), a common measure of diversity (Hill 1973), was also used. Plot area was used as a covariate in analyzing species richness and Simpson's diversity index [N_2] to correct for the known correlation of diversity with plot area (James and Rathbun 1982; Magurran 1988).

TABLE 1. A description of the habitat categories used in this study.

Urban / Rural	Habitat Category	Description
Rural Areas	Forest	Naturally occurring deciduous, coniferous or mixed forest in a rural landscape consisting primarily of natural habitats and farmland.
Rural Areas	Mixed Rural	Plots that include more than one of farmland, successional field, wetland and forest in a rural landscape consisting primarily of natural habitats and farmland.
Rural Areas	Farm	Lands used for crops or pasture with little significant natural vegetation except hedgerows, occurring in a rural landscape consisting of farmland and natural habitats. No farm buildings were present on these plots.
Urban Areas	Urban Natural	Public open spaces with a mixture of natural habitats and horticultural vegetation, surrounded by residential, commercial or industrial areas and located within cities with > 50,000 people. Sites in this category were > 10 ha in extent. The WPBS plot generally occupied the full extent of the natural area or park.
Urban Areas	Urban Natural with Open Water	As for Urban Natural, with open water at least 50 m^2 in extent on a creek, river or pond.
Urban Areas	Small Urban Natural	As for Urban Natural, but ≤10 ha in extent.
Urban Areas	City	Commercial or residential areas within cities or small towns and dominated by buildings and pavement. The sites vary in the density of buildings, the percentage of area covered by pavement and the amount of horticultural vegetation present. Both higher-density urban core areas and lower-density suburban areas are included.

Rarefaction is a technique for comparing collections of items with unbalanced sample sizes, which has always been a problem in measuring ecological diversity (Engstrom and James 1981; James and Rathbun 1982; Brewer and Williamson 1994; Gotelli and Colwell 2001). In this study, the expected number of species in a sample of five birds [$E(S_5)$] was used as the rarefaction index of diversity (James and Rathbun 1982).

Total bird abundance, total land bird abundance and the abundance of each species were assessed as the number of birds per hectare, consistent with standard methods for the Winter Bird Population Study (Kolb 1965; Robbins 1972, 1981). For total abundance, the number of survey hours per hectare was used as a covariate to correct for sampling effort (similar to the suggestion of Bock and Root 1981).

Biomass and average bird size or mass for each plot were calculated in a manner similar to Mauer (1985) using the average mass values for bird species compiled by Dunning (1993). The average mass for each species was multiplied by the average number of birds of that species found on the plot. Total biomass was summed across all species and divided by the plot area in hectares. Similarly, average bird mass was calculated as the total biomass divided by the total number of birds.

The occurrence of birds in different size classes was examined by determining for each plot the percentage of birds in four size classes: < 20 g; 20-40 g; 40-100 g; and > 100 g.

The percentages of birds in different feeding and substrate guilds were estimated using the guild classifications of DeGraaf et al. (1985). Note that a species may be classified in more than one guild. The percentage of field, forest edge and forest species was calculated based on the species' affinities noted by Cadman et al. (1987), Whitcomb et al. (1981), Root (1988), and Freemark and Collins (1992). These are classifications based on breeding season preferences. In this paper I test the applicability of such classifications to winter bird habitat analyses.

Statistical Methods

Analysis of variance was used to test for significant differences in bird community variables among habitat categories. For sites with more than one year of sampling, the mean values for each plot were used to avoid the problem of pseudoreplication (Hulburt 1984). Where departures from the normal distribution and homogeneity of variances could not be overcome through transformation, the non-parametric Kruskal-Wallis analysis of variance test was applied.

Results

Diversity

Bird species richness, Simpson's diversity index (N_2) and the rarefaction diversity index [$E(S_5)$] all differed significantly ($P < 0.0001$, $P < 0.01$ and $P < 0.001$

respectively) among the habitat categories (Table 2). Urban natural areas, forests and mixed habitats showed the highest avian diversity while city and farm showed the lowest diversity (Table 2). Larger urban natural areas (> 10 ha) had diversity indices 5-19% higher than forests.

City areas supported half as many species and about 70% the levels of Simpson's diversity index, N_2, as forests. The rarefaction diversity index [$E(S_5)$] in city areas was about 75% of that for forests. Farmland diversity levels were about one-third those for forests, except the rarefaction diversity index [$E(S_5)$] which was 69% the value for forests. Species richness in mixed rural habitats was about 20% lower than in rural forests, whereas other indices were about as high or higher than values in forests (Table 2).

Abundance, Biomass and Size

Total bird abundance (Table 2) was significantly different ($P < 0.01$) among the habitat categories, due to particularly high abundances in two habitat categories. Total bird abundance was highest in urban natural areas with open water and residential and commercial city areas. Farmland and rural mixed habitats had the lowest levels. Forests and urban natural areas had similar, intermediate levels of bird abundance.

Total bird biomass was significantly different among habitat categories ($P < 0.001$). The highest values were recorded in urban natural areas with open water, due to the presence of waterfowl, and in city areas, due to higher densities and larger species such as the Rock Dove (*Columba livia*). Other urban natural areas and forest had intermediate biomass levels (Table 2).

In urban natural areas with open water, total abundance was 80% higher than in rural forests. Total biomass was 13 times greater in urban natural areas with open water than in rural forests (Table 2). Other urban natural areas showed bird abundance and biomass levels similar to rural forests. Both farms and mixed rural habitats showed abundance levels roughly one third of rural forests. Biomass on farmland was about 30% that in forests while biomass in mixed rural habitats was about 60% of that in forests. Mean bird size was roughly 40% higher in farmland compared with forests. Total bird abundance in cities was 46% higher than that recorded in forests. Biomass was 90-100% higher in cities than in forests.

Significant differences ($P < 0.001$) among habitat categories in the occurrence of birds of different sizes (Figure 1) indicate the cause of the trends of differences in overall biomass shown in Table 2. A preponderance of small bird species (< 20 g) is indicative of forested habitats, as is a relatively even mix of the other size classes. Mixed rural habitats differed from forests primarily in having additional birds in the >100 g class, specifically more raptors. In fact, rural mixed habitats had the highest average bird size. In contrast, city areas showed a preponderance of birds in the intermediate 20-40 gram and 40-100 gram ranges.

TABLE 2. Bird species richness, rarefaction diversity index [$E(S_5)$], Simpson's diversity index [N_2], abundance and biomass levels in seven categories of urban and rural habitats.

Variable		Rural Areas			Urban Areas					
		Farm	Mixed Rural	Forest	Urban Natural	Small Urban Natural	Urban Natural with Open Water	City	Statistical Significance[1]
Species richness	Mean	4.5	12.3	14.7	15.7	7.8	19.2	6.8	****[2]
	Range	4-7	9-15	10-19	10-20	1-16	10-25	3-15	
Rarefaction index of diversity [$E(S_5)$]	Mean	2.42	3.5	3.52	3.69	3.55	2.88	2.66	***
	Range	2.0-3.1	3.5-3.5	3.1-4.0	2.4-4.2	2.4-4.1	1.8-4.3	2.4-3.1	
Simpson's index of diversity (N_2)	Mean	2.3	5.6	5	6.1	3.3	5	3.3	** [2]
	Range	1.3- 2.5	3.6-9.4	4.3-6.9	2.2-9.2	1.0-6.5	1.5-12.5	2.0-3.6	
Total abundance (birds / ha)	Mean	0.72	0.765	2.39	2.46	2.45	4.4	3.5	** [2]
	Range	0.11-1.41	0.25-1.48	1.82-3.57	0.75-4.99	0.31-16.07	1.88-4.37	0.04-6.67	
Biomass (g / ha)	Mean	37.5	92.9	142.4	164.9	111.1	1895	271.3	*** [2]
	Range	4.5-235.1	23.5-333.9	64.0-288.2	52.9-390.5	13.9-677.1	246.5-13,210.9	5.4-899.5	

[1] Statistical significance from Analysis of Variance F-test: * = P < .05; ** = P < .01; *** = P < .001; **** = P < .0001.
[2] Plot area was used as a covariate for species richness and N_2 and sampling effort (hours / ha) as a covariate for abundance and biomass.

The latter category includes the House Sparrow *(Passer domesticus)* and Starling (*Sturnus vulgaris*). Farm areas had a predominance of birds in the 40-100 gram range, which includes the Snow Bunting (*Plectrophenax nivalis*) and Eastern Meadowlark (*Sturnella magna*) (Figure 1).

Guilds

Of food-based feeding guilds, the percentage of insectivorous birds differed most (statistically significance $P < 0.0001$) among habitats (Table 3). Forests, with 25.3 percent, had the highest percentage of insectivores, followed by farms (19.1 percent) and mixed rural habitats (16.7 percent). Cities had only 1.5 percent insectivorous birds. This pattern shows small insectivorous bird species were more indicative of natural, rural forest conditions. Rural mixed habitat shows the highest proportion of carnivorous birds. No significant differences were found among habitat categories for the percentages of omnivores, granivores, herbivores or frugivores (Table 3).

The percentage of four substrate-based guilds differed significantly ($P < 0.01$) among habitat categories (Table 3). Ground-gleaning and foraging species predominated in all urban and farm habitats. Lower canopy species were also important in urban natural areas and rural mixed habitats. In forests, a more even distribution is evident with significant proportions of birds that forage in the upper and lower canopy, on tree trunks and on the ground.

Species Composition

Species showing significant differences ($P < 0.05$) in abundance among the seven habitat categories are shown in Table 4. Of the fifteen most common species only Pine Siskin (*Carduelis pinus*), Evening Grosbeak (*Coccothraustes vespertinus*), and Cedar Waxwing (*Bombycilla cedrorum*) failed to show significant differences among habitat categories, all species subject to periodic extreme peaks in winter abundance (Bock and Lepthien 1976; Root 1988).

Predictably the three alien species — House Sparrow, European Starling and Rock Dove—occurred almost exclusively in city and urban natural areas (Table 4). Some other species reached their greatest abundances in urban natural areas (Table 4), including Mourning Dove (*Zenaida macroura*), American Robin (*Turdus migratorius*), and Northern Cardinal (*Cardinalis cardinalis*).

Species associated with forest edge and fields are the most common in this study. The species American Robin through White-breasted Nuthatch *(Sitta carolinensis)* in Table 4 are generally regarded as either field or forest-edge species. The proportion of forest-edge species is fairly constant at roughly half of birds in forest, mixed rural and urban natural area habitats.

Brown Creeper (*Certhia americana*), Golden-crowned Kinglet (*Regulus satrapa*), Red-breasted Nuthatch (*Sitta canadensis*), Ruffed Grouse (*Bonasa umbellus*), and Hairy Woodpecker (*Picoides villosus*) showed the clearest affinities for forest habitats (Table 4). Fourteen other species generally regarded as forest species during the breeding season occurred at frequencies too low to reveal statistical trends. One third of winter birds recorded in forest areas are regarded as forest species, a much higher percentage than for all other habitats ($P < 0.001$). This analysis suggests that a suite of bird species can be identified that preferentially use forest during winter, as well as during the breeding season.

Differences Among Habitat Categories

A series of significant ecological gradients is revealed in the percentages of small birds, insectivorous species, forest species and alien species across the seven habitat categories in urban and rural southern Ontario. These four variables can be used to summarize the differences in avifauna of the seven habitat categories using multivariate analysis (Table 5). The percentages of birds < 20 g in mass, of insectivorous species, of alien species and of forest species separate

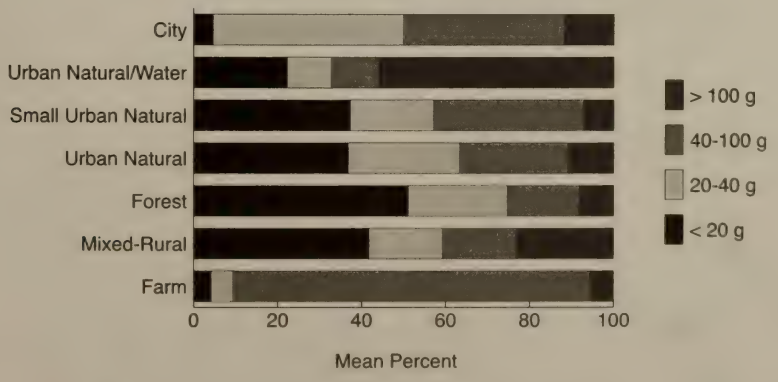


FIGURE. 1. The distribution of birds in four size classes in seven categories of urban and rural habitats. Analysis of variance showed highly significant differences ($P \leq 0.001$).

TABLE 3. Percentages of birds in different guilds in seven categories of urban and rural habitats. [1]

		Rural Areas			Urban Areas				
Guild Type	Guild	Farm	Mixed-Rural	Forest	Urban Natural	Small Urban Natural	Urban Natural with Open Water	City	Statistical Significance[2]
Food	Insectivore	19.1	16.7	25.3	13.9	10.8	10.3	1.5	****
	Carnivore	2.7	10.1	1.4	2.3	3.3	2.5	0.0	*
	Omnivore	20.4	39.4	38.3	43.8	53.1	52.2	41.1	
	Granivore	50.1	33.2	35.5	42.7	35.8	33.6	56.4	
	Frugivore	6.0	9.8	15.3	8.2	7.2	8.1	2.5	
	Herbivore	3.5	3.4	3.5	0.7	0.4	2.6	0	
Substrate	Upper Canopy	0.0	16.6	34.9	12.4	7.0	7.6	13.8	***
	Lower Canopy	10.3	43.9	46.2	35.2	31.0	30.7	3.6	**
	Ground	72.6	46.9	35.3	63.7	68.4	68.0	94.6	***
	Bark	19.1	15.8	23.6	13.4	10.7	10.5	0.9	***

[1] Note that numbers for each guild type in each column do not sum to 100% as some species may be members of more than one guild (see DeGraaf et al. 1985).
[2] Statistical significance from Kruskal-Wallis Test is: * = P < .05; ** = P < .01; *** = P < .001; **** = P < .0001.

the seven habitat categories in a non-parametric, Epanechnikov kernel discriminant analysis (Hand 1982). The technique successfully categorized 96.2 percent of the 52 plots ($P < 0.0001$). Only two plots were mis-categorized and these were two urban natural area plots classified in one of the other two categories of urban natural areas.

Discussion

Patterns revealed here regarding winter bird species richness and diversity in urban and rural habitats were similar to other studies in different climatic zones (Lancaster and Rees 1979; DeGraaf and Wentworth 1981, 1986; Tilghman 1987; Adams 1994). Diversity was higher in forest, rural mixed habitats and urban natural areas compared with cities and farms. Tilghman (1987) found species richness in an urban area in Massachusetts, U.S. was only 50% of that in forests and a similar finding is reported here, in a colder region with more consistent snow cover.

In northern and temperate ecosystems, bird species richness and abundance are lower in winter than summer (Anderson et al. 1981; Morrison et al. 1987). The magnitude of the seasonal difference in avian diversity and abundance also differs among habitats. Some studies show that in winter, birds favor areas with greater vegetation cover compared to summer (Morrison et al. 1987, western U.S.) and areas with milder microclimates (Shields and Grubb 1976, north central U.S.). Urban areas provide larger, more stable food supplies, higher temperatures and reduced temperature variability which may result in higher avian productivity and survival rates (Marzluff et al. 1998).

Total bird abundance and biomass were highly variable and differences among habitat categories did not explain much of the variance. The presence of water and riparian bird species had a major influence on total avian abundance in this study. Waterfowl are known to move into cities in the winter due to the higher temperatures and resulting open water (Tilghman 1987; Gilbert 1989; Adams 1994). The occasional occurrence of flocks of northern finches has been noted as a possible cause of low explanatory power of habitat variables related to bird abundance (Tilghman 1987). Intra-species and inter-species flocking, known to be important in winter bird assemblages (e.g., Berner and Grubb 1985; Morrison et al. 1987), might also contribute to greater variability. Abundance is also affected by landscape effects at larger scales than individual study plots (Pearson 1993; Hostletler and Holling 2000).

The differences in the sizes of birds present in different habitat categories are remarkable and this has not been examined to any extent in North America. Hostletler and Holling (2000) found that birds of different sizes responded to the amount of urban forest cover at different scales. In this study, smaller birds (< 20 g) favored forests, mixed rural habitats and

TABLE 4. Densities of individual species in seven categories of urban and rural habitats. Values shown are birds per hectare.

		Rural Areas			Urban Areas				
Species	Species' Habitat Affinities[2]	Farm	Mixed-Rural	Forest	Urban Natural	Small Urban Natural	Urban Natural with Open Water	City	Significance[1]
House Sparrow *Passer domesticus*	Urban				0.206	0.462	0.084	1.503	****
European Starling *Sturnus vulgaris*	Urban		0.01		0.387	0.638	0.296	0.819	***
Rock Dove *Columba livia*	Urban		0.013		0.001		0.044	0.307	***
American Robin *Turdus migratorius*	Field				0.021	0.001	0.069	0	*
Mourning Dove *Zenaida macroura*	Field		0		0.145	0.104	0.050		**
American Tree Sparrow *Spizella arborea*	Field		0.079	0.044	0.105	0.048	0.014		*
American Goldfinch *Carduelis tristis*	Field		0.091	0.23	0.273	0.523	0.072	0.025	**
Song Sparrow *Melospiza melodia*	Forest Edge		0.01	0.006	0.058	0.001	0.033		**
Red-tailed Hawk *Buteo jamaicensis*	Forest Edge	0.004	0.024	0.004	0.019	0.020	0.010		***
Black-capped Chickadee *Poecile atricapillus*	Forest Edge	0.005	0.191	0.610	0.406	0.851	0.269	0.086	**
Downy Woodpecker *Picoides pubescens*	Forest Edge	0.006	0.053	0.154	0.144	0.271	0.087	0.009	***
Dark-eyed Junco *Junco hyemalis*	Forest Edge			0.079	0.205	0.276	0.087	0.006	**
Northern Cardinal *Cardinalis cardinalis*	Forest Edge		0.01	0.019	0.164	0.243	0.070	0.028	***
Blue Jay *Cyanocitta cristata*	Forest Edge		0.025	0.175	0.103	0.115	0.036	0.011	***
White-breasted Nuthatch *Sitta carolinensis*	Forest Edge		0.026	0.133	0.074	0.114	0.046	0.029	*
Hairy Woodpecker *Picoides villosus*	Forest	0.007	0.025	0.095	0.018	0.068	0.024	0.002	*
Brown Creeper *Certhia americana*	Forest		0.038	0.081	0.016	0.004	0.016	0.001	**
Golden-crowned Kinglet *Regulus satrapa*	Forest		0.025	0.044	0.007	0.002			***
Red-breasted Nuthatch *Sitta canadensis*	Forest			0.125	0.007	0.010			*
Ruffed Grouse *Bonasa umbellus*	Forest		0.051	0.076		0.001	0.002		****

[1] Statistical significance from Kruskal-Wallis Test is: * = P < .05; ** = P < .01; *** = P < .001; **** = P < .0001.
[2] Classification based primarily on Cadman et al. 1987.

TABLE 5. Percentages of alien, forest, insectivorous and small bird species in seven categories of urban and rural habitats. A non-parametric, Epanechnikov kernel discriminant analysis correctly categorized 96.2 percent of the 52 plots as to habitat classification using these four variables ($P < 0.0001$).

Variable	Rural Areas			Urban Areas			
	Farm	Mixed-Rural	Forest	Urban Natural	Small Urban Natural	Urban Natural with Open Water	City
Percentage Alien Species	0.0	1.9	0.0	21.2	22.1	27.4	80.4
Percentage Forest Species	19.1	21.7	37.9	19.9	14.5	13.9	1.5
Percentage Insectivores	18.0	17.7	33.3	12.3	9.4	8.4	1.2
Percentage Small Bird Species (< 20 g)	4.2	41.7	51.1	36.8	37.3	22.3	4.6

urban natural areas. Larger birds, 20-100 g in size, were prevalent in cities and on farms. Marzluff et al. (1998) speculated that urbanization likely favours ground foraging bird species and discourages canopy and bark foragers. Ground-foraging birds characteristic of open country are generally larger than species foraging on branches in woodland habitats (e.g., Polo and Carrascal 1999). More complex forested habitats are thought to provide greater opportunities for small birds foraging among branches and milder microclimates, especially protection from wind. Woodlands may support a larger variety of sizes of wintering bird species as observed in this study.

Both cities and farms favor a small number of granivorous and omnivorous species (Møller 1984; O'Connor and Shrubb 1986; Lack 1992; Adams 1994; Marzluff et al. 1998). The volume of food available to birds in some cities is enormous, perhaps more than the entire bird assemblage would require (Lancaster and Rees 1979). Raptor populations are sometimes lower in cities (Tomialojc 1982; Adams 1994) and this study suggests this may be the case in southern Ontario. In this study, granivorous and omnivorous birds were ubiquitous in all habitats, consistent with the available winter food. Significant variation in the proportion of insectivores across the habitat categories was a major trend noted in this study and one variable that best distinguishes the seven habitat categories.

The identification of species' preferences during summer for field, forest edge and forest has been widespread (Whitcomb et al. 1981; Ambuel and Temple 1983; Robbins et al. 1989; Freemark and Collins 1992). But investigation of species' preferences during winter has been more limited (Blake 1987; Tilghman 1987; Telleria and Santos 1995). This study corroborates preliminary work in the northern United States on species' preferences during winter (Blake 1987, Illinois; Tilghman 1987, Massachusetts) and suggests a broader trend across several climatic zones. Many of the species associated with forest, forest edge and field during summer show similar preferences during winter.

Some interesting new findings arise from analysis of winter bird use of urban and rural habitats in southern Ontario, as well as corroboration and extension of results from a few other studies of winter bird use in the northern U.S. (Blake 1987; Tilghman 1987). Small, insectivorous and forest species were prevalent in forests while larger, ground feeding and omnivorous birds overwhelmingly dominated cities and farms. Urban natural areas occupy an intermediate point on this gradient from natural rural forests to most human-modified sites on farms and in cities. Granivorous and omnivorous species dominated all habitat categories. Variation in the abundance of small, insectivorous, upper and lower canopy and forest bird species was one of the major sources of variance in this study. Trends in biomass and bird sizes suggest further research on these aspects of winter bird communities.

The different habitat categories can be successfully classified based on the percentages of small species, insectivores, forest species and alien species using multivariate discriminant analysis. More research on winter bird use of farmland habitats in North America would be useful given the patterns found in European work. Additional work measuring species preferences in winter for forest, forest-edge and field habitats would also be useful given the interesting results so far.

Acknowledgments

Thanks are extended to the volunteers who conducted the winter bird population studies used in this paper. The Toronto Bird Observatory, James L. Baillie Fund and Toronto Field Naturalists, supported many of these field studies. John Theberge provided support and guidance at early stages of this research. Mike Cadman, Paul Eagles, Anthony Erskine, George Francis, John Theberge and anonymous reviewers provided comments on drafts of the manuscript.

Literature Cited

Adams, L. 1994. Urban wildlife habitats: a landscape perspective. University of Minneapolis Press, Minneapolis.

Ambuel, B., and **S. Temple**. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64: 1057-1068.

Anderson, B., **R. Ohmart**, and **J. Rice**. 1981. Seasonal changes in avian densities and diversities. Pages 262-264 *in* Estimating the Numbers of Terrestrial Birds. *Edited by* C. Ralph and J. Scott. Studies in Avian Biology 6.

Berner, T., and **T. Grubb**. 1985. An experimental analysis of mixed-species flocking in birds in deciduous woodland. Ecology 66: 1229-1236.

Bignal, E., and **D. McCraken**. 1996. Low-intensity farming systems in the conservation of the countryside. Journal of Applied Ecology 33: 413-424.

Blake, J. 1987. Species-area relationships of winter residents in isolated woodlots. Wilson Bulletin 99: 243-250.

Bock, C., and **L. Lepthien**. 1976. Synchronous eruptions of boreal seed-eating birds. American Naturalist 110: 559-571.

Bock, C., and **T. Root**. 1981. The Christmas Bird Count and avian ecology. Pages 17-23 *in* Estimating the Numbers of Terrestrial Birds. *Edited by* C. Ralph and J. Scott. Studies in Avian Biology 6.

Brady, R., **T. Tobias**, **P. Eagles**, **R. Ohrner**, **J. Micak**, **B. Weale**, and **R. Dorney**. 1979. A typology for the urban ecosystem and its relationship to larger biogeographical landscape units. Urban Ecology 4: 11-28.

Brewer, A., and **M. Williamson**. 1994. A new relationship for rarefaction. Biodiversity and Conservation 3: 373-379.

Cadman, M., **P. Eagles**, and **F. Helleiner**. 1987. Atlas of the breeding birds of Ontario. University of Waterloo Press, Waterloo, Canada.

Campbell, C., and **A. Dagg**. 1976. Bird populations in downtown and suburban Kitchener-Waterloo, Ontario. Ontario Field Biologist 30: 1-22.

DeGraaf, R., and **J. Wentworth**. 1981. Urban bird communities and habitats in New England. Transactions of the North American Wildlife and Natural Resources Conference 46: 396-413.

DeGraaf, R., and **J. Wentworth**. 1986. Avian guild structure and habitat associations in suburban bird communities. Urban Ecology 9: 399-412.

Degraaf, R., **N. Tilghman**, and **S. Anderson**. 1985. Foraging guilds of North American birds. Environmental Management 9: 493-536.

Dunning, J. 1993.The CRC handbook of avian body masses. CRC Press, Boca Raton, Florida.

Engstrom, R., and **F. James**. 1981. Plot size as a factor in winter-bird population studies. Condor 83: 34-41.

Erskine, A. 1992. A ten-year urban winter bird count in Sackville, New Brunswick. Canadian Field-Naturalist 106: 499-506.

Erskine, A. 1980. Urban birds in the context of Canadian climate and settlement. Pages 1321-1326 *in* Symposium on Urbanization. *Edited by* R. Murton and M. Luniak. Proceedings of the 17th International Ornithological Congress. Berlin, Germany.

Erskine, A. 1975. Winter birds of urban residential areas in eastern Canada. Pages 18-31 *in* Nature and Urban Man. *Edited by* G. McKeating. Canadian Nature Federation, Special Publication Number 4.

Freemark, K., and **B. Collins**. 1992. Landscape ecology of birds breeding in temperate forest fragments. Pages 443-454 *in* Ecology and management of Neotropical Migrant Landbirds. *Edited by* J. Hagan and D. Johnson. Smithsonian Press, Washington.

Gilbert, O. 1989. The ecology of urban habitats. Chapman and Hall, London.

Gotelli, N., and **R. Colwell**. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391.

Hand, D. 1982. Kernel discriminant analysis. Research Studies Press, New York.

Hill, M. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427-432.

Hinsley, S., **P. Bellamy**, **I. Newton**, and **T. Sparks**. 1996. Influences of population size and woodland area on bird species distributions in small woods. Oecologia 105: 100-107.

Hochachka, W., **J. Wells**, **K. Rosenberg**, **D. Tessaglia-Hymes**, and **A. Dhondt**. 1999. Irruptive migration of common redpolls. Condor 101: 195-204.

Hohtola, E. 1978. Differential changes in bird community structure with urbanization: a study in central Finland. Ornis Scandinavica 9: 94-100.

Hostletler, M., and **C. Holling**. 2000. Detecting the scales at which birds respond to structure in urban landscapes. Urban Ecosystems 4: 25-54.

Hulburt, S. 1984. Pseudoreplication and the design of ecological experiments. Ecological Monographs 54: 187-211.

James, F., and **S. Rathbun**. 1982. Rarefaction, relative abundance, and diversity of avian communities. Auk 98: 785-800.

Kolb, H. 1965. The Audubon winter bird population study. Audubon Field Notes 19: 432-434.

Lack, P. 1992. Birds on lowland farms. HMSO, London.

Lancaster, R., and **W. Rees**. 1979. Bird communities and the structure of urban habitats. Canadian Journal of Zoology 57: 2358-2368.

Magurran, A. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

Marzluff, J., **F. Gehlbach**, and **D. Manuwal**. 1998. Urban environments: influences and challenges for the avian conservationist. Pages 283-299 *in* Avian Conservation:

Research and Management. *Edited by* J. Marzluff and R. Sallabanks. Island Press, Washington, D.C.

Mauer, B. 1985. Avian community dynamics in desert grasslands: observational scale and hierarchical structure. Ecological Monographs 55: 295-312.

Mehlman, D. 1997. Change in avian abundance across the geographic range in response to environmental change. Ecological Applications 7: 614-624.

Møller, A. 1984. Community structure of birds in agricultural areas in summer and winter in Denmark. Holarctic Ecology 7: 413-418.

Morneau, F., **M. St-Georges**, **D. Lambert**, et **J.-L DesGranges**. 1996. Assemblages d'oiseaux en hiver dans des parc urbains de 39 villes des basses-terres du St. Laurent : richesse, habitat et comparaison biogéographique. G.R.E.B.E. inc. pour Environnement Canada. Série de rapports techniques (258). Service canadien de la faune, Région du Québec.

Morrison, M., **K. With**, **I. Timossi**, and **K. Milne**. 1987. Composition and temporal variation of flocks in the Sierra Nevada. Condor 89: 739-745.

Newton, I. 1998. Bird conservation problems resulting from agricultural intensification in Europe. Pages 307-322 *in* Avian Conservation: Research and Management. *Edited by* J. Marzluff and R. Sallabanks. Island Press, Washington, D.C.

Nour, N., **R. Van Damme**, **E. Matthysen**, and **A. Dhondt**. 1999. Forest birds in forest fragments: are fragmentation effects independent of season? Bird Study 46: 279-288.

O'Connor, R., and **M. Shrubb**. 1986. Farming and birds. Cambridge University Press, Cambridge, U.K.

Parrish, T., **K. Lakhani**, and **T. Sparks**. 1994. Modelling the relationship between bird population variables and hedgerow and other field margin attributes. I. Species richness of winter, summer and breeding birds. Journal of Applied Ecology 31: 764-775.

Pearson, S. 1993. The spatial extent and relative influence of landscape level factors on wintering bird populations. Landscape Ecology 8: 3-18.

Polo, V., and **L. Carrascal**. 1999. Shaping the body size distribution of passeriformes: habitat use and body size are evolutionarily and ecologically related. Journal of Animal Ecology 68: 324-337.

Robbins, C. 1972. An appraisal of the winter bird population study technique. American Birds 26: 688-692.

Robbins, C. 1981. Reappraisal of the Winter Bird Population Study technique. Pages 52-57 *in* Estimating the Numbers of Terrestrial Birds. *Edited by* C. J. Ralph and J. M. Scott. Studies in Avian Biology 6.

Robbins, C., **D. Dawson**, and **B. Dowell**. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildlife Monographs (103).

Rodenhouse, N., **L. Best**, **J. O'Connor**, and **E. Bollinger**. 1995. Effects of agricultural practices and farmland structures. Pages 269-293 *in* Ecology and Management of Neotropical Migratory Birds, A Synthesis and Review of Critical Issues. *Edited by* T. Martin and D. Finch. Oxford University Press, Oxford, United Kingdom.

Root, T. 1988. Atlas of wintering birds of North America: an analysis of Christmas bird count data. University of Chicago Press, Chicago.

Saunders, D., **R. Hobbs**, and **C. Margules**. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5: 18-32.

Shields, W., and **T. Grubb**. 1976. Winter bird densities on north and south slopes. Wilson Bulletin 86: 125-130.

Smith, P. 1984a. Observer and annual variation in winter bird population studies. Wilson Bulletin 96: 561-574.

Smith, P. 1984b. Winter birds of small urban woodlots in Kitchener-Waterloo. American Birds 38: 60-61.

Smith, P., **G. Fairfield**, **D. Burton**, and **D. Knauber**. 1982. Winter bird communities of urban southern Ontario. American Birds 36: 46-47.

Smith, P., **D. Knauber**, **D. Ulster**, **D. Banville**, **J. MacDonald**, **G. Fairfield**, and **D. Burton**. 1981. Winter bird communities of selected areas in Toronto. American Birds 35 :41-44.

Telleria, J., and **T. Santos**. 1995. Effects of forest fragmentation on a guild of wintering passerines: the role of habitat selection. Biological Conservation 71: 61-67.

Tilghman, N. 1987. Characteristics of urban woodlands affecting winter bird diversity and abundance. Forest Ecology and Management 21: 163-175.

Tomialojc, L. 1982. Synurbization of birds and the prey-predator relations. Pages 131-140 *in* Animals in Urban Environment. *Edited by* M. Luniak and B. Pisarski, Polish Academy of Sciences, Warsaw.

Whitcomb, R., **C. Robbins**, **J. Lynch**, **B. Whitcomb**, **M. Klimkiewicz**, and **D. Bystrak**. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-205 *in* Forest Island dynamics in man-dominated landscapes. *Edited by* R. Burgess and D. Sharpe. Springer Verlag, New York.

Wilson, W. 1994. The distribution of wintering birds in central Maine: the interactive effects of landscape and bird feeders. Journal of Field Ornithology 65: 512-519.

Received 14 December 2000
Accepted 29 October 2003

APPENDIX. The 52 Winter Bird Population Study plots in southern Ontario used in this paper.

Site #	Site Name	Region County/	Area (ha)	Site #	Site Name	Region County/	Area (ha)
1	Chats Falls	Ottawa-Carleton	8.4	25	Nordheimer Ravine	Toronto	10.1
2	Purpleville A	York	17.4	26	Wigmore Ravine	Toronto	34.0
3	Chesney Bog	Oxford	15.2	27	Sherwood Park	Toronto	18.5
4	St. Lawrence Island National Park	Leeds	12.5	28	Waterloo Park A	Waterloo	24.3
5	Purpleville B	York	10.5	29	Blockline/ Strasbourg	Waterloo	1.2
6	Rondeau Provincial Park	Kent	6.1	30	Campus Woodlot	Waterloo	0.8
7	South Walsingham	Haldimand-Norfolk	10.1	31	Salt Spring Road	Waterloo	0.7
8	Flamboro area	Hamilton-Wentworth	41.7	32	Upper Gerrard Ravine	Toronto	5.0
9	Homer Watson	Waterloo	10.1	33	Old Country Road	Waterloo	0.7
10	Dundas area	Hamilton-Wentworth	6.3	34	Village Woods	Waterloo	0.7
11	Acton area	Halton	4.9	35	Hidden Valley	Waterloo	1.2
12	Victoria Park	Waterloo	22.9	36	Chatsworth Ravine	Toronto	4.4
13	Waterloo Park B	Waterloo	24.3	37	Mabel Davis	York	6.5
14	Bayview Woods	Toronto	20.0	38	Rockway Gardens	Waterloo	2.3
15	Cootes Paradise	Hamilton-Wentworth	13.0	39	Downtown Waterloo	Waterloo	25.0
16	Riverside Park	Waterloo	81.0	40	Downtown Ottawa	Ottawa-Carleton	41.0
17	Steckle Woods	Waterloo	26.2	41	Westboro/ Highland	Ottawa-Carleton	111.0
18	Moore Park	Toronto	13.2	42	Kent/Percy	Ottawa-Carleton	50.6
19	Strathgowan Woods	Toronto	8.1	43	Hemlock/ Hickory	Waterloo	25.0
20	Cedarvale Ravine	Toronto	20.0	44	Guelph	Wellington	4.0
21	Rosedale Valley	Toronto	19.4	45	Carleton Place	Ottawa-Carleton	103.0
22	Park Drive	Toronto	19.6	46	Alta Vista	Ottawa-Carleton	97.1
23	Lakeside Park	Waterloo	14.2	47	Copeland/Belair	Ottawa-Carleton	111.0
24	Humber River - Land	Toronto	10.9	48	Rockcliffe Park	Ottawa-Carleton	87.0
				49	Beechwood	Waterloo	25.0
				50	Vaughan A	York	20.2
				51	Carp River	Ottawa-Carleton	70.8
				52	Vaughan B	York	40.5

Field Identification of the Mice *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* in Central New York

Erin Stewart Lindquist[1], Charles F. Aquadro[2], Deedra McClearn[3], and Kevin J. McGowan[4]

Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA
Current addresses:
[1] Organization for Tropical Studies, Apartado 676-2050, San Pedro, Costa Rica
[2] Department of Molecular Biology & Genetics, Cornell University, Corsan Hall, Biotechnology Building, Ithaca, New York 14853 USA
[3] Pennsylvania State University, P.O. Box 598, Lemont, Pennsylvania 16851 USA
[4] Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14850 USA

Lindquist, Erin Stewart, Charles F. Aquadro, Deedra McClearn, and Kevin J. McGowan. 2003. Field identification of the mice *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* in central New York. Canadian Field-Naturalist 117(2): 184-189.

Field identification of the White-footed Mouse (*Peromyscus leucopus noveboracensis*) and Long-tailed Deer Mouse (*Peromyscus maniculatus gracilis*) is difficult because of their similar external morphology. *Peromyscus* were sampled by live-trapping during a five-year period (1992-1996) at the Arnot Teaching and Research Forest, Van Etten, New York and identified to species by electrophoresis of their salivary amylase. No electromorphs were shared between *P. leucopus* and *P. maniculatus*, thus permitting unambiguous species identification of individuals. Means and ranges of four external measurements (ear, head-body, hind-foot, and tail) and tail to head-body ratio were determined for amylase-genotyped live mice. Although some body measurements did differ on average between the two species (ear, head-body, and tail for adults; hind-foot and tail for juveniles), the ranges of these overlap considerably. When the four external measurements (excluding the tail to head-body ratio) were used to construct two discriminant-function equations, they yielded correct identification of 80% of the adult *P. l. noveboracensis* and *P. m. gracilis* assessed excluding juveniles, and 71% of adult and juvenile mice combined. The function reported here allows partial field identification, but genetic analysis remains the only reliable field method for differentiation between live *P. l. noveboracensis* and *P. m. gracilis*.

Key Words: *Peromyscus leucopus*, *Peromyscus maniculatus*, identification, salivary amylase, external characters, discriminant-function.

In the northeastern United States and southeastern Canada, the Deer Mouse, *Peromyscus maniculatus*, and the White-footed Mouse, *Peromyscus leucopus*, are sympatric over a large portion of their ranges (Klein 1960; Smith and Speller 1970; Grant 1976; Parren and Capen 1985; Garman et al. 1994; Long 1996). In regions where the White-footed Mouse, *P. l. noveboracensis*, and the long-tailed subspecies of the Deer Mouse, *P. m. gracilis*, are both present, field identification has proven to be difficult.

Characteristics of the tail and pelage have been cited as useful in differentiating the two species (Osgood 1909; Choate 1973; Whitaker and Hamilton 1998). Choate (1973) found that *P. l. noveboracensis* has a tail to head-body length ratio of < 1, whereas *P. m. gracilis* has a ratio that approaches or exceeds 1. Several researchers, however, have reported that external phenotypic characteristics in the field are unreliable (Grant 1976; Feldhamer et al. 1983; Palas et al. 1992; Garman et al. 1994; Rich et al. 1996; Sternburg and Feldhamer 1997; Kamler et al. 1998; Bruseo et al. 1999).

Discriminant-function equations using cranial measurements to distinguish between *P. l. noveboracensis* and *P. m. gracilis* have been constructed (Choate 1973; Long and Long 1993; Rich et al. 1996; Sternburg and Feldhamer 1997), but this method requires the sacrifice of individuals, and thus is not useful for on-going ecological studies. Stromberg (1979) developed a discriminant-function with field measurements for separating *P. l. noveboracensis* and *P. m. bairdii* in southern Wisconsin, but this function can not be used to discriminate between the two long-tailed subspecies. For identification of *P. l. noveboracensis* and *P. m. gracilis*, Garman et al. (1994) developed a discriminant-function equation with the tail-to-body length ratio as the independent variable, but they did not report the equation or its ability to discriminate between species. Feldhamer et al. (1983) and Sternburg and Feldhamer (1997) constructed discriminant-functions using only external characteristics of *P. l. noveboracensis* and *P. m. gracilis* and classified 98.6% of the *Peromyscus* correctly. Their measurements, however, were taken from dead individuals and thus are more accurate than is possible with live mice. Finally, Bruseo et al. (1999) used external field measurements in a discriminant analysis to differentiate *P. l. noveboracensis* and *P. m. nubiterrae* in the Appalachian Mountains. Although their models correctly classified up to 92% of live individuals, the authors concluded that electrophoresis of salivary amylase is the only technique that provides unambiguous identification of these two subspecies.

Peromyscus maniculatus and *P. leucopus* have unique salivary amylase variants and therefore can be accurately identified by their amylase allozyme genotype (Aquadro and Patton 1980). Aquadro and Patton's (1980) approach has been employed successfully in various ecological studies of eastern *Peromyscus* to improve the accuracy of field identifications (Feldhamer et al. 1983; Merriam et al. 1989; Palas et al. 1992; Garman et al. 1994; Rand et al. 1993; Kilpatrick et al. 1994; Rich et al. 1996; Sternburg and Feldhamer 1997; Bruseo et al. 1999). Several researchers have concluded that identification of *P. maniculatus* and *P. leucopus* in northeastern North America can be reliably done only using molecular markers (Feldhamer et al. 1983; Palas et al. 1992; Kilpatrick et al. 1994; Rich et al. 1996; Sternburg and Feldhamer 1997). Because identification with salivary amylase is time consuming and requires an extensive laboratory analysis, a method for quick field identification would be beneficial for mark-recapture studies.

The primary objective of this study was to improve field identification of *P. leucopus noveboracensis* and *P. maniculatus gracilis* for field studies and to extend the results of Bruseo et al. (1999) to another geographic location with a different subspecies of *P. maniculatus*. *Peromyscus* live-trapped in central New York State over a five-year period were identified to species through electrophoretic analysis of their salivary amylase. We also examined the usefulness of external and measured characters cited previously for the identification of these two sympatric species. We then statistically tested the trend cited by Choate (1973) for tail to head-body length ratio of each species. In addition, two discriminant classification equations were derived from four external body measurements of all individuals discerned to species by the electrophoretic analysis.

Methods

Field Methods

Peromyscus leucopus noveboracensis and *P. maniculatus gracilis* were live-trapped on three study plots in the Arnot Teaching and Research Forest of Cornell University, Van Etten, New York, USA (42° 17' 30" N, 76° 40' 00" W; altitude= 500-550 m). The two species are known to dwell in forests in the northeastern United States, northern Michigan, Wisconsin, and southeastern Canada, and are often sympatric (Hamilton 1943; Baker 1983; Whitaker and Hamilton 1998). The Prairie Deer Mouse, *P. m. bairdii*, also has been trapped previously in Tompkins Co., New York (the northeasternmost part of the subspecies' range) in open field habitats (Whitaker and Hamilton 1998). From our tail measurements of trapped *P. maniculatus*, we are certain all our specimens belong to the *P. m. gracilis* subspecies.

Two of the trapping plots were in un-mowed pasture (old field habitat), and the other was located in a transition forest that was logged in the early 1900s and dominated by red maple (*Acer rubrum*) and beech (*Fagus grandifolia*). One hundred Sherman live traps were spaced 5 m apart in 10 by 10 grids in each plot. As part of a mark-recapture study, the plots were trapped from late May to early November of 1992-96 for two nights each week. Traps were open between 1800 and 0600 hrs with two trap checks (1200 and 0600 hrs) each night.

All mammals captured alive were identified to genus, weighed, measured, and sexed. We took quantitative body measures of each *Peromyscus* at first capture only. We recorded tail length, head-body length, ear length, and hind-foot length to the nearest mm using a clear, flexible plastic ruler. At first capture we collected a saliva sample (Aquadro and Patton 1980). Field assistants did not attempt to identify *Peromyscus* to species in the field.

Laboratory Methods

We genotyped saliva samples for salivary amylase using Aquadro and Patton's (1980) electrophoretic method. A known sample from the *Peromyscus* Stock Center with the Amy-1^{100} electromorph of *P. leucopus* was added to each gel as a standard (Dawson and Ward 1994); amylase electromorphs were then designated by percentage mobility relative to Amy-1^{100} mobility. The Amy-1^{100} electromorph is only found in *P. leucopus* (Aquadro and Patton 1980).

Statistical Analyses

We genotyped only those samples with distinct bands. Once the species of each individual was determined electrophoretically, differences between the body measurements of each species could be reliably assessed. All 220 *P. maniculatus* and *P. leucopus* identified to species from the five years and three trapping plots were grouped together in their respective species and age groups for our statistical analyses. We chose weight as the determining factor for age because it reflects the relative size of the individual. We classified an individual as an adult if it weighed $\geq$ 15 g, and as a juvenile if it weighed < 15 g (Wolff 1985). We used two-tailed Student's *t*-tests to compare the adult and juvenile lengths of the tail, head-body, hind-foot, ear, and tail to head-body ratio between each species (MINITAB Inc. 1995). In addition, within each species we compared the tail and head-body lengths of each individual mouse with a paired *t*-test.

We developed two discriminant-function equations: one for adults, and one for adults and juveniles combined (SYSTAT Inc. 1992). We used four variables: tail length, head-body length, hind-foot length, and ear length. The discriminant analysis optimally weights the four body measurement variables to segregate the two species. The discriminant-functions can be used to predict the species of new, unclassified individuals.

Results

We collected 270 salivary amylase samples from individuals trapped in the three plots over five years (1992-1996). Of these, 220 samples had sufficient

amylase for electrophoresis. In 55 of the samples analyzed, we found enzymatic degradation that made distinguishing between homozygotes and heterozygotes at the amylase locus difficult (probably due to thawing and refreezing during transportation and storage). In these cases species identification was unambiguous, but exact genotype was not scored. Thus, we identified 220 individuals to species, and scored the genotypes of 165 individual *Peromyscus*.

We found two salivary amylase electromorphs, Amy-1^{76} and Amy-1^{85}, in frequencies of 81.7% and 18.3% (N= 186) respectively that were unique to *P. maniculatus*. *P. leucopus* carried two different alleles, Amy-1^{94} and Amy-1^{100}, which we found at frequencies of 88.2% and 11.8% (N= 144).

P. maniculatus gracilis was significantly larger than *P. leucopus noveboracensis* in head-body, tail, and ear lengths for adults and juveniles (Table 1). Tail lengths for adults and juveniles of *P. maniculatus* were significantly longer than those for *P. leucopus* (t = -9.47, d.f. = 148, $P < 0.0001$; and t = -3.02, d.f. = 67, $P = 0.004$ respectively). The head-body lengths for adult *P. maniculatus* were significantly longer than that of *P. leucopus* (t = -4.98, d.f. = 149, $P < 0.001$), but the juvenile head-body lengths between species were not (t = -1.33, d.f. = 67, $P = 0.19$). The ear lengths of adult *P. maniculatus* also were significantly longer than those of adult *P. leucopus* (t = -3.58, d.f. = 145, $P < 0.001$), whereas the ear lengths of juvenile *P. maniculatus* were not longer than those of *P. leucopus* (t = -1.44, d.f. = 67, $P = 0.16$). Adult hind-foot lengths did not differ between species (t = -0.586, d.f. = 149, $P = 0.56$), but juvenile *P. maniculatus* had longer hind-feet than *P. leucopus* (t = -1.08, d.f. = 67, $P < 0.001$).

For both the adult and juvenile groups of *P. m. gracilis* and *P. l. noveboracensis*, tail length of an individual mouse was found to be greater than head-body length (paired t-test; = -10.4, d.f. = 98, $P < 0.001$ for *P. maniculatus* adults; t = -3.20, d.f. = 50, $P = 0.0024$ for *P. leucopus* adults; t = -7.08, d.f. = 51, $P < 0.0001$ for *P. maniculatus* juveniles; and t = -3.43, d.f. = 16, $P = 0.0034$ for *P. leucopus* juveniles). The individual tail to head-body ratio on *P. maniculatus* was significantly greater than the ratio for *P. leucopus* in adults, but not for juveniles (t = -2.44, d.f. = 149, $P < 0.016$ for adults; and t = -1.56, d.f. = 67, $P = 0.12$ for juveniles). Both ratios were on average equal to or greater than 1 (Table 1).

The first pair of discriminant-function equations (Table 2a), constructed for adults, classified 80.1% (117 of 146 total) of the *Peromyscus* into their correct species groups (Figure 1a). Of 97 *P. maniculatus* tested, 21 (21.6%) were misidentified, and of 49 *P. leucopus*, 8 (16.3%) were not classified correctly.

The addition of juveniles in the discriminant-function lowered its success rate. The second pair of equations (Table 2b) constructed with adults and juveniles, classified 71.6% (154 of 215 total) of the *Peromyscus*

TABLE 1. Measurements of four morphological measurement variables and the tail to head-body ratio for *P. l. noveboracensis* and *P. m. gracilis*, near Van Etten, New York in 1992-1996. Significance values refer to interspecies, within age comparisons by t-tests and are noted at larger mean value.

Length (mm)	*P. maniculatus*						*P. leucopus*					
	Juvenile			Adult			Juvenile			Adult		
	$\bar{X}$	SD	range	$\bar{X}$	SD	range	$\bar{X}$	SD	range	$\bar{X}$	SD	range
Ear	14.6	2.7	7-23	15.3***	2.3	10-21	13.6	2.4	9-17	13.9	2.0	9-17
Hind-Foot	18.7***	1.6	11-21	19.2	1.4	16-22	18.2	1.7	15-20	19.0	1.5	15-23
Head-Body	67.3	6.4	53-80	74.1***	6.9	58-94	64.9	6.4	52-75	68.5	5.8	54-86
Tail	76.5**	7.3	51-88	84.1***	7.2	70-105	70.3	7.9	57-90	72.2	7.4	50-88
Tail/ Head-Body	1.15	0.15	0.77-1.47	1.13***	0.14	0.88-1.55	1.09	0.11	0.88-1.38	1.06	0.13	0.82-1.49
Sample size (n)[a, b]	52			100			17			51		

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

[a] Ear length values are for 98 and 49 adult *P. maniculatus* and *P. leucopus* respectively because of missing data.

[b] *P. maniculus* tail length values are for 99 mice only.

TABLE 2. Group classification coefficients for discrimination between *P. l. noveboracensis* and *P. m. gracilis* using external characteristics from N=220 individuals caught near Van Etten, New York in 1992-1996.

	a. Adults only		b. Adults and Juveniles	
Variable	*P. leucopus* n= 49	*P. maniculatus* n= 97	*P. leucopus* n= 66	*P. maniculatus* n= 149
Ear	1.205	1.331	0.552	0.668
Head-body	1.301	1.405	0.812	0.849
Hind-foot	9.642	9.724	7.263	7.231
Tail	1.388	1.608	0.889	1.033
Constant	-195.810	-223.871	-132.300	-146.965

correctly (Figure 1b). Of 149 *P. maniculatus* tested, 44 (29.5%) were misidentified, whereas of 66 *P. leucopus*, 17 (25.8%) were not classified correctly.

Discussion

We were able to identify unambiguously individuals captured as *P. leucopus noveboracensis* or *P. maniculatus gracilis* using salivary amylase genotype. No electromorphs were shared between the two species. We found both species to be polymorphic at the amylase locus. The alleles found in our study (Amy-1^{76} and Amy-1^{85} for *P. maniculatus*, and Amy-1^{94} and Amy-1^{100} for *P. leucopus*) were consistent with those found in previous studies (Aquadro and Patton 1980; Feldhamer et al. 1983; Merriam et al. 1989; Palas et al. 1992; Kilpatrick et al. 1994; Rich et al. 1996; Sternburg and Feldhamer 1997; Bruseo et al. 1999). Aquadro and Patton (1980) reported only the Amy-1^{76} and the Amy-1^{100} in their New York *P. maniculatus* and *P. leucopus*, respectively, but had assayed only four individuals of each species. Our larger sample size allowed us to detect the less frequent alleles in *P. leucopus* and *P. maniculatus*.

Our ranges for lengths of tail for *P. l. noveboracensis* and *P. m. gracilis* were similar to previously reported values (Godin 1977; Baker 1983; Whitaker and Hamilton 1998). We found that hind-foot length was not a reliable distinguishing characteristic for the two species as also suggested by others (Baker 1983; Feldhamer et al. 1983; Palas et al. 1992; Whitaker and Hamilton 1998). Ear lengths were more variable than other reported ranges, and have resulted from the difficulties measuring live mice in the field (Baker 1983; Feldhamer et al. 1983; Sternburg and Feldhamer 1997).

Although *P. m. gracilis* were on average larger than *P. l. noveboracensis*, their body measurements overlapped considerably making identification difficult (Table 1). For example, tail lengths of adult *P. leucopus* range from 50-88 mm, whereas tail lengths of adult *P. maniculatus* range from 70-105 mm. In the range of 70-88 mm, a mouse could be classified as a member of either species if tail length was used as the sole identification characteristic. Furthermore, the area of overlap in body measurements is greater for ear, hind-foot, and head-body lengths than for tail length. Tail to head-body ratio values of the two species also overlapped considerably (Table 1). If body dimensions were solely used to identify *Peromyscus*, ambiguous identifications would thus be obtained.

FIGURE 1A

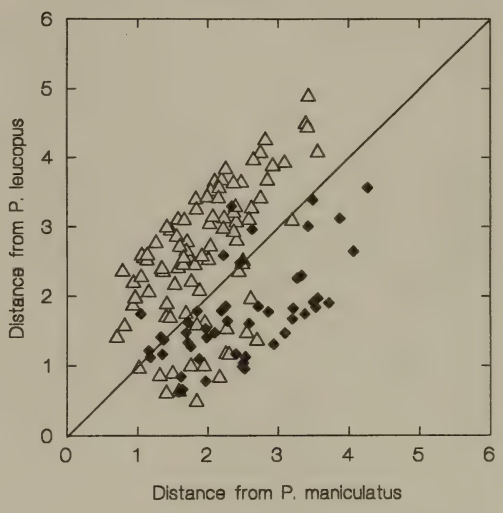


FIGURE 1B

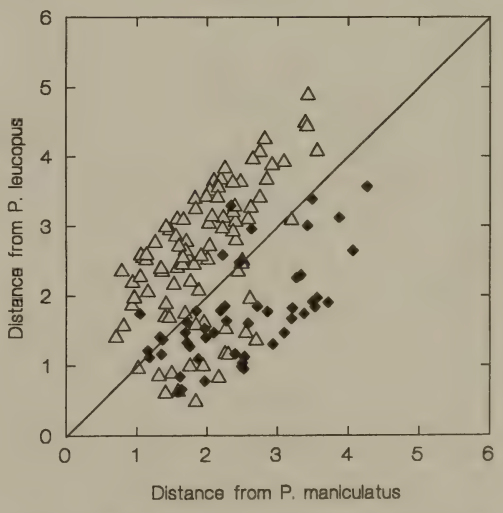


FIGURE 1. Classification of *P. l. noveboracensis* and *P. m. gracilis* using the discriminant-function coefficients given in Table 2. Figure 1a shows the classification of adults only. Figure 1b shows the classification of adults and juveniles. Open and closed symbols denote *P. m. gracilis* and *P. l. noveboracensis*, respectively. In Figure 1b, *P. m. gracilis* is indicated by open circles and squares (adult and juvenile, respectively), and *P. l. noveboracensis* by closed triangles and stars (adult and juvenile, respectively).

Choate (1973) reported that the tail to head-body ratio was valuable for species identification of *P. l. noveboracensis* and *P. m. gracilis*, with *P. l. noveboracensis* having a ratio < 1. Although the ratio was larger for *P. m. gracilis* than *P. l. noveboracensis* in our study, the two species had ratios ≥ 1 (Table 1). In previous studies where head-body lengths were taken from dead specimens, the average tail to head-body ratios for both species were < 1, although *P. l. noveboracensis* had larger ratios than either *P. m. bairdii* or *P. m. nubiterrae* (Feldhamer et al. 1983; Sternburg and Feldhamer 1997). We found that the tail to head-body ratio is not a diagnostic characteristic for the field identification of *P. l. noveboracensis* and *P. m. gracilis* in central New York as did Bruseo et al. (1999).

Juvenile *Peromyscus* demonstrated the same trends observed in adult *Peromyscus* for tail, and tail to head-body length ratio. When juveniles were included with adults in the second discriminant-function equation, the success rate of the classification function decreased (Figure 1b). Some researchers have been concerned with including juveniles in their discriminant-functions or standard *t*-tests. Palas et al. (1992) reported that misidentification using body measurements is most probable in the young age classes. Choate (1973) excluded juveniles when constructing his discriminant-function. On the other hand, Rich et al. (1996) included juveniles in their function even though significant differences were found between age classes within species. We agree with Rich et al.'s (1996) reasoning that the purpose of a discriminant-function analysis is to construct a function that classifies all specimens to species independent of age or size.

The discriminant-function reported here will enable researchers to partially differentiate between the two species in a live-trapping study. Yet we also have confirmed the unreliability of identifications that depend solely on external characteristics. While our discriminant-functions are an improvement from the independent external measurements and tail to head-body ratio, they still have a degree of ambiguity. Unambiguous identification of live *P. l. noveboracensis* and *P. m. gracilis* in the field still appears to be only possible by genetic analysis.

Acknowledgments

We thank the numerous field assistants who allowed this project to continue for its five years, especially Amy Heusinkveld for her enthusiasm. Live-traps and field vehicles were provided by Milo Richmond, and by the Department of Natural Resources and the Section of Ecology and Systematics, Cornell University. We also thank Martha Hamblin and the entire Aquadro lab for assisting with the amylase analysis. C. William Kilpatrick, Robert Timm, and several anonymous reviewers provided helpful comments on earlier manuscript versions. The field work was supported by USDA McIntire-Stennis project NYC-183559 to D.M. The laboratory analysis was supported by the Division of Biological Sciences Undergraduate Honors Program, Cornell University.

Literature Cited

Aquadro, C. F., and **J. C. Patton.** 1980. Salivary amylase variation in *Peromyscus*: use in species identification. Journal of Mammalogy 61: 703-707.

Baker, R. H. 1983. Michigan Mammals. Michigan State University Press, Detroit.

Bruseo, J. A., S. H. Vessey, and **J. S. Graham.** 1999. Discrimination between *Peromyscus leucopus noveboracensis* and *Peromyscus maniculatus nubiterrae* in the field. Acta Theriologica 44: 51-160.

Choate, J. R. 1973. Identification and recent distribution of white-footed mice (*Peromyscus*) in New England. Journal of Mammalogy 54: 41-48.

Dawson, W. D., and **O. G. Ward.** 1994. The *Peromyscus* genetic stock center. *Peromyscus* Newsletter 17: 7-10.

Feldhamer, G. A., J. E. Gates, and **J. H. Howard.** 1983. Field identification of *Peromyscus maniculatus* and *P. leucopus* in Maryland: reliability of morphological characteristics. Acta Theriologica 28: 417-423.

Garman, S. L., A. F. O'Connell, Jr., and **J. H. Connery.** 1994. Habitat use and distribution of the mice *Peromyscus leucopus* and *P. maniculatus* on Mount Desert Island, Maine. Canadian Field-Naturalist 108: 67-71.

Godin, A. J. 1977. Wild mammals of New England. The Johns Hopkins University Press, Baltimore, Maryland.

Grant, P. R. 1976. An 11-year study of small mammal populations at Mont St. Hilaire, Quebec. Canadian Journal of Zoology 54: 2156-2173.

Hamilton, W. J., Jr. 1943. The mammals of eastern United States. Comstock Publishing Company, Ithaca, New York.

Kamler, J. F., D. S. Pennock, C. Welch, and **R. J. Pierotti.** 1998. Variation in morphological characteristics of the white-footed mouse (*P. leucopus*) and the deer mouse (*P. maniculatus*) under allotopic and syntopic conditions. American Midland Naturalist 140: 70-179.

Kilpatrick, C. W., S. M. Rich, and **K. L. Crowell.** 1994. Distribution of the genus *Peromyscus* in coastal and inland-southwestern Maine. Maine Naturalist 2: 1-10.

Klein, H. G. 1960. Ecological relationships of *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* in central New York. Ecological Monographs 30: 387-407.

Long, C. A. 1996. Ecological replacement of the deer mouse, *Peromyscus maniculatus*, by the white-footed mouse, *P. leucopus*, in the Great Lakes Region. Canadian Field-Naturalist 110: 271-277.

Long, C. A., and **J. E. Long.** 1993. Discriminant analysis of geographic variation in long-tailed deer mice from northern Wisconsin and Upper Michigan. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 81: 107-121.

Merriam, G., M. Kozakiewicz, E. Tsuchiya, and **K. Hawley.** 1989. Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes. Landscape Ecology 2: 227-235.

MINITAB, Inc. 1995. MINITAB Version 10.5. MINITAB, Inc., USA.

Osgood, W. H. 1909. Revision of the mice of the American genus *Peromyscus*. North American Fauna 28: 1-285.

Palas, J. S., O. A. Schwartz, and **A. M. Vivas.** 1992. Identification of Iowa *Peromyscus* using external measurements and salivary amylase. Prairie Naturalist 24: 273-277.

Parren, S. G., and **D. E. Capen.** 1985. Local distribution and coexistence of two species of *Peromyscus* in Vermont. Journal of Mammalogy 66: 36-44.

Rand, P. W., E. H. Lacombe, R. P. Smith, Jr., S. M. Rich, C. W. Kilpatrick, C. A. Dragoni, and **D. Caporale.** 1993. Competence of *Peromyscus maniculatus* (Rodentia: Cricetidae) as a reservoir host for *Borrelia burgdorferi* (Spirochaetares: Spirochaetaceae) in the wild. Journal of Medical Entomology 3: 614-618.

Rich, S. M., C. W. Kilpatrick, J. L. Shippee, and **K. L. Crowell.** 1996. Morphological differentiation and identification of *Peromyscus leucopus* and *P. maniculatus* in northeastern North America. Journal of Mammalogy 77: 985-991.

Smith, D. A., and **S. W. Speller.** 1970. The distribution and behavior of *Peromyscus maniculatus gracilis* and *Peromyscus leucopus noveboracensis* (Rodentia: Cricetidae) in a southeastern Ontario woodlot. Canadian Journal of Zoology 48: 1187-1199.

Sternburg, J. E., and **G. A. Feldhamer.** 1997. Mensural discrimination between sympatric *Peromyscus leucopus* and *P. maniculatus* in southern Illinois. Acta Theriologica 42: 1-13.

Stromberg, M. R. 1979. Field identificat188ion of *Peromyscus leucopus* and *P. maniculatus* with discriminant analysis. Transactions of the Wisconsin Academy of Sciences, Arts, and Letters 67: 159-164.

SYSTAT, Inc. 1992. SYSTAT: Statistics, Version 5.2 Edition. SYSTAT, Inc., Evanston, Illinois.

Whitaker, J. O. Jr., and **W. J. Hamilton.** 1998. Mammals of the eastern United States, 3rd edition. Comstock Publishing Associates, Cornell University Press, Ithaca, New York.

Wolff, J. O. 1985. The effects of density, food, and interspecific interference on home range size in *Peromyscus leucopus* and *Peromyscus maniculatus*. Canadian Journal of Zoology 63: 2657-2662.

Received 3 January 2001
Accepted 7 October 2003

Assessing an American Marten, *Martes americana*, Reintroduction in Vermont

Trina L. Moruzzi[1, 2], Kimberly J. Royar[3], Clayton Grove[4], Robert T. Brooks[2], Christopher Bernier[3], Frank L. Thompson, Jr.[5], Richard M. DeGraaf[2], and Todd K. Fuller[1]

[1] Department of Natural Resources Conservation, University of Massachusetts, Amherst, Massachusetts 01003-4210 USA
[2] US Forest Service, Northeastern Research Station, Amherst, Massachusetts 01003-4210 USA
[3] Vermont Department of Fish and Wildlife, Springfield, Vermont 05156 USA
[4] US Forest Service, Green Mountain National Forest, Rutland, Vermont 05701 USA
[5] US Forest Service, Green Mountain National Forest, Manchester, Vermont 05255 USA

Moruzzi, Trina L., Kimberly J. Royar, Clayton Grove, Robert T. Brooks, Christopher Bernier, Frank L. Thompson, Jr., Richard M. DeGraaf, and Todd K. Fuller. 2003. Assessing an American Marten, *Martes americana*, reintroduction in Vermont. Canadian Field-Naturalist 117(2): 190-195.

During October-December 1989-1991, biologists from the Vermont Fish and Wildlife Department and the USDA Forest Service reintroduced 115 (88 male, 27 female) American Martens (*Martes americana*) into the southern half of the Green Mountain National Forest. During the years of release, brief radio-contact was made with 9 of the 13 (8 male, 5 female) radio-collared animals, and several of these may have established residency. Results of winter track count surveys suggested the presence of at least four Martens in 1990. During winter 1994-1995, Trailmaster® cameras and boxed camera systems detected Martens at two, and Fishers (*Martes pennanti*) at 11, of 20 sites. During winter 1997-1998, Fishers were detected at 37 of 47 boxed camera sites, but no Martens were detected. During summer 1997 and 1998, no Marten photos were recorded at 285 pressure-plate camera stations in a larger area that included all Marten release sites. Although post-release monitoring may have been insufficient to definitively confirm Marten presence, results from the 1997 and 1998 camera surveys indicate that a viable population of Martens was not established in southern Vermont, perhaps due to competition with Fishers.

Key Words: Fisher, *Martes pennanti*, American Marten, *Martes americana*, carnivores, reintroduction, camera, survey, Vermont.

Beginning in the 1600s, American Martens (*Martes americana*) largely were extirpated from their southern ranges, particularly east and south of the Great Lakes (Gibilisco 1994). In response, numerous Marten reintroductions to former habitats (n = 38) and introductions to new range (n = 7) have occurred since 1934 (Slough 1994). Though many of these were deemed "successful", at least seven were failures, mostly due to small numbers of animals involved (Slough 1994).

Historically, Martens also occurred throughout Vermont, but extensive deforestation and unregulated trapping from the late 1800s through the early 1900s led to their decline and eventual extirpation (DiStefano et al. 1990*). Because Martens are classified as endangered by the Vermont Fish and Wildlife Department (VFWD), a recovery plan was implemented by the VFWD and the US Forest Service (USFS) to restore at least two viable populations in suitable habitats within the State (DiStefano et al. 1990*). If these populations became established (>300 individuals/population), their legal status could be changed from endangered to threatened (DiStefano et al. 1990*).

Initially, wild-trapped Martens from Maine and New York were to be translocated to northeastern and southern areas in Vermont, but the northeastern site was abandoned due to local political pressure. During October-December 1989-1991, the VFWD and the USFS reintroduced Martens at two sites in the southern portion of the Green Mountain National Forest (GMNF) in southern Vermont (Royar 1992*). This paper reviews the attempts made during 1989-1995 to assess the success of the Marten reintroduction, presents new information on extensive remote-camera surveys conducted during winter 1997-1998 and summers 1997 and 1998, and gives an overall assessment of the likelihood of a viable population of Martens occurring in southern Vermont.

Marten Releases

In each of the three release years, 31-40 Martens were released near Manchester, Vermont (Figure 1; 43°N, 73°W) using either a quick or slow release method (Table 1). All Martens (n = 115; 88 male, 27 female; 104 from Maine, 11 from New York) were tagged in each ear with individually numbered tags, and 13 (8 male, 5 female) of them also were fitted with radiocollars. In November 1989, five other unmarked male Martens escaped from their transport cages 25 km east of the release site. Relocation efforts ended in 1991 after the total number of females released (n = 27) neared the original goal of 30 (Trombulak and Royar 2001).

All releases occurred at relatively high elevations within the Green Mountains (~650 m and ~785 m in the northern and southern release areas, respectively) where Fishers were less likely to be encountered (Kelly

* See Documents Cited Section.

FIGURE 1. Location of two areas where Martens were released during October-December 1989-1991 (circled areas); Marten track count transects, January-March 1990 (dashed lines); track plates, 1990 (triangles); camera stations winter 1994-1995 (open circles); camera stations winter 1997-1998 (closed circles), and extent of the area surveyed with camera stations during summers 1997 and 1998 (heavy solid line) in and near the Green Mountain National Forest and the town of Manchester, southern Vermont.

TABLE 1. Ratios of adult and juvenile male and female Martens that were released during reintroduction attempts in the Green Mountain National Forest, southern Vermont (Royar 1992*).

Ratio	1989	1990	1991	Total
Adult:Juvenile	35:5	26:5	30:14	91:24
Male:Female	29:11	25:6	34:10	88:27
Slow:Quick[a]	12:28	8:23	20:24	40:75
Total	40(6)[b]	31(7)	44(0)	115(13)

[a] Quick release method involved releasing Martens as soon as they were transported to the release site; slow release involved keeping Martens in holding boxes for several days at the site before release.
[b] Number of Martens wearing radio collars.

1977) in predominantly spruce and fir cover types. Northern hardwoods were also common in the area, but little cleared land or herbaceous cover occurred at the release site locations (Royar 1992*). Monthly (December-March) snow depth averaged about 37 cm during 1990-1998 at a 510-m elevation site within southern GMNF (Northeast Regional Climate Center, Ithaca, New York).

In December each year, a two-week trapping season for Fishers was open in the study area, and all pelts and carcasses were required to be registered. The density of drivable roads and trails in the eastern half of the study area was about 0.9 km/km^2 vs. 1.6 km/km^2 in the west.

Assessment

Telemetry monitoring

In winter 1989-1990 radio contact was made with three of six radio-collared Martens, but actual locations of individuals were not identified due to time and accessibility constraints (Royar 1992*). In 1990-1991, six of seven radio-collared Martens were located from the ground and the air one to six times each, and though four individuals seemed to settle and perhaps establish home ranges near the release sites, the others were never located within 10 km of the release area. On 31 March 1991 efforts to locate lost animals using aerial telemetry were unsuccessful, and telemetry efforts were terminated.

Snow tracking and sooted track plates

Snow tracking conditions during January-February 1990 surveys (Figure 1) ranged from excellent to very poor, although tracks of 1-2 Martens and those of 0-2 individuals of other carnivores were observed on each survey (Table 2). No more than four Martens could be accounted for at any one time on the three different transects (two on Transect 1, and one each on Transects 2 and 3). Two sooted track plates were set out for two weeks during December 1992 (Figure 1), but no Martens (or any other species) were detected because snow hardened on top of the track plates before any animal walked on them.

Initial remote camera surveys

During October 1994-January 1995, 20 remotely triggered Trailmaster® (TM) cameras were paired (≥30 m apart) with 20 camera boxes and set out near four former release sites (Figure 1) in an attempt to definitively identify any Marten in the area (Brooks 1996). TM camera systems tripped by animals breaking an infrared beam (Kucera and Barrett 1993) were attached to wooden frames anchored 2 m above the ground on a convenient tree bole, and aimed at a climbing pole baited with skunk-essence lure and a meat bait. Automatic cameras in 81×23×23-cm wooden boxes tripped by animals stepping on an aluminum treadle at the entrance (cf., Danielson et al. 1996) were set 2 m above the ground and attached to a tree bole. Camera boxes were baited with Beaver (*Castor canadensis*) meat, Marten gland lure, and a skunk essence lure. Cameras were operational for 60-75 days.

One photo of a Marten was taken at a camera box at one site; photos of Martens also were taken at another site 9.6 km away at both the paired TM and camera-box stations (Brooks 1996). Photos of Fishers were taken by both camera box and TM cameras at six and nine of the stations, respectively (Table 3), and at a total of 11 different sites.

Remote camera survey, winter 1997-1998

During January-March 1998, 47 baited camera boxes were placed a minimum of 1 km apart within 8 km of Marten release sites (Figure 1), and above 550 m

TABLE 2. Tracks of Martens and other carnivores observed in snow on surveys conducted during winter 1990 in the Green Mountain National Forest, southern Vermont (Royar 1992*).

Transect	Length (km)	Date	Tracking conditions	Time since last snowfall	Number of individual Martens identified	Number of individuals of other species identified
1	12.9	3 January	excellent	thawed and refrozen 48 hrs prior to survey	2	1 Fisher
		8 February	poor	96 h	1	
		22 February	excellent-poor	48 h	2	
2	9.7	25 January	fair-poor	24 h; rained during survey	1	1 Fisher
3	1.6	22 February	very poor	60 h since 50-cm snowfall; started snowing during survey	1	1 Bobcat 2 Coyote 1 Red Fox

TABLE 3. Proportion of remote Trailmaster® (TM) camera and camera box (BOX) stations at which various species were photographed during winter in the Green Mountain National Forest, southern Vermont. In 1994-1995, paired TM and BOX cameras were located within ≤30m of one another (Brooks 1996 and unpublished data).

Species	1994-1995 (n = 20)[a]		1998 (n = 47)[b]
	TM	BOX	BOX
Fisher (*Martes pennanti*)	0.45	0.30	0.79
American Marten (*Martes americana*)	0.05	0.10	0.00
Bobcat (*Lynx rufus*)	0.00	0.00	0.04
Long-tailed Weasel (*Mustela frenata*)	0.00	0.00	0.02
Ermine (*Mustela erminea*)	0.05	0.00	0.00
Black Bear (*Ursus americanus*)	0.00	0.00	0.02
Raccoon (*Procyon lotor*)	0.00	0.00	0.02
Flying Squirrel (*Glaucomys* spp.)	0.60	0.15	0.00
Red Squirrel (*Tamiasciurus hudsonicus*)	0.50	0.05	0.00
Blue Jay (*Cyanocitta cristata*)	0.15	0.00	0.00
Peromyscus spp.	0.05	0.00	0.00
Human	0.00	0.00	0.06

[a] Cameras set for 60-80 days each.
[b] Cameras set for 45-70 days each.

elevation where Fishers purportedly were less likely to be encountered (Kelly 1977). Camera locations included all areas surveyed by Brooks (1996) in 1995, plus additional sites in the Forest. Camera boxes were operational for 40-65 days.

No Martens were detected, but Fishers were photographed at 37 of the 47 camera sites (Table 3). During winter 1998, Fishers were detected in every area surveyed during the 1995 study, and in the areas where Martens were detected during 1995. Several other carnivore species were photographed during 1998, as well.

Remote camera survey, summer 1997 and 1998

During the summers of 1997 and 1998, a broader carnivore distribution study using remote cameras was conducted in a 1032-km^2 area in and immediately adjacent to the Green Mountain National Forest (Figure 1; Moruzzi et al. 2002). Cameras were placed at 1-km intervals at 131 and 154 baited trap stations in 1997 and 1998, respectively. We photographed Martens at no stations, but Fishers at 47 stations, during the two summers.

Other reports

A report from Candia, New Hampshire confirmed that a Marten released seven months earlier (i.e., with appropriate ear tags) was road-killed there in June 1990 — 145 km east of its release site. Another released in November 1989 was trapped in a Fisher set in December 1990 in Shrewsbury, Vermont — 15 km north of its release site. A third marked Marten was road-killed in nearby (15 km) Winhall, Vermont in 1991, and a fourth near Bakersville, Connecticut in June 1992 — 160 km south of its 1990 release site. A fifth marked Marten was trapped in Rangeley, Maine in November 1997 — 245 km northeast of its 1989 release site.

Discussion

The goal of the Marten reintroduction project was to establish at least two viable populations of Martens in Vermont. Despite the release of 115 animals, track count surveys in 1990 suggested the presence of no more than four Martens (Royar 1992*), and photos taken in winter 1994-95 confirmed the presence of no more than two (Brooks 1996). In addition, our more extensive camera surveys during winter 1997-1998 and summers of 1997 and 1998 failed to detect any Martens. Given the data that were collected, there is no evidence that Martens have established a viable population in the area.

The success of Marten reintroduction efforts, as well as those of other carnivores, appears to depend on several factors (Berg 1982; Slough 1994; Reading and Clark 1996; Breitenmoser et al. 2001). In the Vermont reintroduction, many of these factors do not seem to be responsible for the apparent failure of the project. First, an adequate number of individuals is essential. In Vermont, relatively few females were released each year, but the final total (27) was near the target number of 30 (cf., Slough 1994), and this was more than were released in at least 15 successful reintroductions or introductions. Also, releases conducted over several years, such as was done in Vermont, versus a single release seem preferable (Slough 1994). Additionally, a male-biased sex ratio may increase the likelihood of establishing a normal spacing pattern and maximize reproductive success (Slough 1994); again, this was the case in Vermont. Martens also should be wild-caught and from areas similar to the area to which animals are moved (Slough 1994); animals moved to Vermont were from nearby New York and Maine. Martens also should be protected from trapping, but even though Fisher trapping was allowed in the area for a short period each winter, the small

number of Martens reported trapped over a large area over many years indicates that trapping was not an important mortality factor.

Habitat suitability might strongly influence translocation success of Martens. Prior to the release in Vermont, GMNF stand inventory data were compared with Marten-specific habitat suitability models (e.g., Allen 1982), and some fieldwork was conducted to assess percent softwood, tree size class, and dead and downed material (Trombulak and Royar 2001). These efforts suggested that the proportion of softwood canopy closure might have been relatively low, but there is no particular reason to believe that these vegetation characteristics would limit Marten survival (Chapin et al. 1997:715). However, such stand-level attributes might not be nearly as relevant as landscape level configuration (Chapin et al. 1998, Hargis et al. 1999). Although no such landscape evaluation has been carried out, most such concerns focus on the effects of extensively logging on habitat fragmentation. Since levels of logging in the GMNF have been very low for the past 20 years, we do not suspect that such considerations affected Marten populations.

Another factor that might limit Marten reintroduction success is interspecific competition, particularly with Fishers (Slough 1994). Abundance of the two species often has been reported to be inversely proportional, perhaps reflecting the dynamics of food competition and/or predation by Fishers on Martens (Krohn et al. 1995, 1997). In Vermont, all releases occurred at relatively high elevations where Fishers were thought to be less abundant. Still, the high rate of Fisher photos, in particular, that we obtained suggested that they had become more common in the area than previously believed. Fisher pelt prices and corresponding trapper effort dropped significantly in the late 1980s, likely resulting in a statewide increase in Fisher numbers (K. Royar, unpublished data). Also, deep and frequent snowfalls apparently limit Fisher abundance and distribution (Krohn et al. 1995, 1997). In our area, long periods of thick snow typical of the study area previous to the translocation (mean number of days snow thicker than 46 cm during December-March 1979-1988 = 34) was less common in the years immediately following the release (mean number of days snow deeper than 46 cm during December-March 1989-1998 = 23; Vermont Department of Fish and Wildlife). Thus, a general increase in Fisher numbers because of reduced trapping pressure and in Fisher distribution in the Marten release area because of reduced snowfall may have limited the success of the Marten reintroduction, albeit by unknown means.

Conclusions

While the initial attempts to assess the success of the Marten reintroduction in southern Vermont were limited, the results of our most recent winter survey suggest that few if any individuals survived to establish a viable population. The reasons for this outcome are not clear, but undocumented competition with Fishers seems to be the most workable one.

It seems clear that the previous surveys were inadequate to document the occurrence of resident Martens in Vermont. In any future attempt to restore Martens in Vermont, a landscape level analysis of habitat seems prudent. When Martens are released, more extensive and definitive winter track count and track plate surveys should be conducted, and additional camera stations (Bull et al. 1992; Jones and Raphael 1993; Raphael 1994) should be set in and near sighting areas to provide definitive evidence of Marten presence. Perhaps most importantly, more radiomarked animals should be monitored intensively and extensively, as well, especially to monitor the fates of Martens and to keep up with widely moving individuals. Concomitantly, a more intensive effort to monitor Fisher abundance, distribution, and interactions with Martens is necessary. Apparently no Marten translocations have been carried out in areas with high Fisher densities, and the actual mechanisms by which Fishers might limit Martens have not been documented.

Documents Cited (marked * in text)

DiStefano, J. J., K. J. Royar, D. M. Pence, and **J. E. Denoncour**. 1990. Marten recovery plan for Vermont. Vermont Fish and Wildlife Department, Waterbury, Vermont. 19 pages.

Royar, K. J. 1992. Monitoring reintroduced marten populations in Vermont. Vermont Fish and Wildlife Department, Waterbury, Vermont. 33 pages.

Literature Cited

Allen, A. W. 1982. Habitat suitability index models: martens. U.S. Fish and Wildlife Service. FWS/OBS-82/10.11.

Berg, W. E. 1982. Reintroduction of fisher, pine marten, and river otter. Pages 159-173 *in* Midwest Furbearer Management. *Edited by* G. C. Sanderson. Symposium Proceedings. 43rd Midwest Fish and Wildlife Conference, Wichita, Kansas.

Breitenmoser, U., C. Breitenmoser, L. N. Carbyn, and **S. M. Funk.** 2001. Assessment of carnivore reintroductions. Pages 241-281 *in* Carnivore conservation. *Edited by* J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne. Cambridge University Press, Cambridge, United Kingdom.

Brooks, R. T. 1996. Assessment of two camera-based systems for monitoring arboreal wildlife. Wildlife Society Bulletin 24: 298-300.

Bull, E. L., R. S. Holthausen, and **L. R. Bright.** 1992. Comparison of 3 techniques to monitor marten. Wildlife Society Bulletin 20: 406-410.

Chapin, T. G., D. J. Harrison, and **D. M. Phillips.** 1997. Seasonal habitat selection by marten in an untrapped forest preserve. Journal of Wildlife Management 61: 707-717.

Chapin, T. G., D. J. Harrison, and **D. D. Katnik.** 1998. Influence of landscape pattern on habitat use by American marten in an industrial forest. Conservation Biology 12:1327-1337.

Danielson, W. R., R. M. DeGraaf, and **T. K. Fuller**. 1996. An inexpensive compact automatic camera system for wildlife research. Journal of Field Ornithology 67: 414-421.

Gibilisco, C. J. 1994. Distributional dynamics of modern *Martes* in North America. Pages 59-71 *in* Martens, Sables, and Fishers: Biology and Conservation. *Edited by* S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell. Cornell University Press, Ithaca, New York.

Hargis, C. D., J. A. Bissonette, and **D. L. Turner.** 1999. The influence of forest fragmentation and landscape pattern on American martens. Journal of Applied Ecology 36: 157-172.

Jones, L. C., and **M. G. Raphael**. 1993. Inexpensive camera systems for detecting martens, fishers, and other animals: guidelines for use and standardization. U.S. Forest Service, General Technical Report PNW-306.

Kelly, G. M. 1977. Fisher (*Martes pennanti*) biology in the White Mountain National Forest and adjacent areas. Ph.D. Dissertation, University of Massachusetts, Amherst. 178 pages.

Krohn, W. B., K. D. Elowe, and **R. B. Boone**. 1995. Relations among fishers, snow, and martens: development and evaluation of two hypotheses. The Forestry Chronicle 71: 97-105.

Krohn, W. B., W. J. Zielinski, and **R. B. Boone**. 1997. Relations among fishers, snow, and martens in California: results from small-scale spatial comparisons. Pages 211-232 *in Martes*: taxonomy, techniques, and management. *Edited by* G. Proulx, H. N. Bryant, and P. M. Woodard. Provincial Museum of Alberta, Edmonton, Canada.

Kucera, T. E., and **R. H. Barrett**. 1993. The Trailmaster® camera system for detecting wildlife. Wildlife Society Bulletin 21: 505-508.

Moruzzi, T. L., T. K. Fuller, R. M. DeGraaf, R. T. Brooks, and **W. Li**. 2002. Assessing remotely triggered cameras for surveying carnivore distribution. Wildlife Society Bulletin 30: 380-386.

Raphael, M. G. 1994. Techniques for monitoring populations of fishers and martens. Pages 224-240 *in* Martens, Sables, and Fishers: Biology and Conservation. *Edited by* S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell. Cornell University Press, Ithaca, New York.

Reading, R. P., and **T. W. Clark**. 1996. Carnivore reintroductions: an interdisciplinary examination. Pages 296-336 *in* Carnivore behavior, ecology, and evolution, volume 2. *Edited by* J. L. Gittleman. Cornell University Press, Ithaca, New York.

Slough, B. G. 1994. Translocations of American martens: an evaluation of factors in success. Pages 165-178 *in* Martens, Sables, and Fishers: Biology and Conservation. *Edited by* S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell. Cornell University Press, Ithaca, New York.

Trombulak, S. C., and **K. Royar**. 2001. Restoring the wild: species recovery and reintroduction. Pages 157-181 *in* Wilderness comes home: rewilding the Northeast. *Edited by* C. M. Klyza. University Press of New England, Hanover, New Hampshire.

Received 26 February 2001
Accepted 30 October 2003

Seasonal Dynamics and Defoliation Impact on Herbage Yield in Aspen Boreal Habitats of Alberta

NOBLE T. DONKOR[1], MOSES M. OKELLO[1], ROBERT J. HUDSON[1,3] AND EDWARD W. BORK[2]

[1]Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2H1 Canada
[2]Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Alberta T6G 2P5 Canada
[3]Corresponding Author: E-mail: robert.hudson@ualberta.ca

Donkor, Noble T., Moses M. Okello, Robert J. Hudson, and Edward W. Bork. 2003. Seasonal dynamics and defoliation impact on herbage yield in aspen boreal habitats of Alberta. Canadian Field-Naturalist 117 (2): 196-202.

Within the aspen boreal ecosystems, little information exists on the seasonal dynamics of available herbage and the effects of varying defoliation regimes on accumulated herbage growth and associated opportunities for animal production. We examined seasonal changes in herbage phytomass in conjunction with defoliation treatments in *Bromus inermis-Poa pratensis* grasslands in central Alberta. Changes in herbage pools were examined by sampling at five monthly intervals from April to September 1997 and 1998, inclusive. Vegetation was also subjected to a factorial experiment with an initial defoliation in late-May, June or July, at heights of 2.5, 7.5, or 15 cm, and repeated at 3-, 6- or 9-week intervals until the end of September. Green herbage, standing dead and fallen litter increased from spring to summer and decreased from summer to fall. Average growing conditions resulted in a peak phytomass of 350 g m^{-2}, and varied by year. Weathering losses of green herbage, standing dead and fallen litter over winter were 34%, 52% and 51%, respectively. Dry matter losses of total herbage (all three pools) over winter were 58% of 1997 summer green phytomass. Initial timing, height, and frequency of clipping all affected accumulated herbage yield ($P < 0.001$). The greatest accumulated herbage yield was from clipping initiated in May. Light clipping resulted in less phytomass accumulation relative to moderate and heavy clipping. Clipping frequencies of six and nine weeks resulted in similar phytomass removal, but were greater than herbage removal associated with three weeks frequency. The interaction between clipping date and frequency of clipping demonstrates the importance of temporal rest and sensitivity of forage plants to defoliation, and lends support to the use of rotational grazing systems.

Key Words: herbage production, bromegrass, *Bromus inermis*, bluegrass, *Poa pratensis*, defoliation.

The Aspen Parkland and Low Boreal Mixedwood ecoregions form a gradual transitional zone in central Alberta between southern prairie and northern boreal forests (Rowe 1972; Strong 1992). Landscapes within the region largely consist of a patchwork mosaic of Trembling Aspen (*Populus tremuloides*) and Balsam Poplar (*Populus balsamifera*) forests alternating with grasslands (McCartney 1993; Bork et al. 1997). These areas contain forage resources suited to supporting beef enterprises, diversified livestock and free-ranging native ungulates (Telfer and Scotter 1975; Baron and Knowles 1984). Over the last century, this area has been increasingly influenced by European settlement and agricultural expansion resulting in significant alterations to the physiognomy of many forests and introduction of many non-native forage species such as Smooth Bromegrass (*Bromus inermis*) and Kentucky Bluegrass (*Poa pratensis*). Despite the abundance of these introduced perennial grass species, little information is available on the seasonal dynamics of available herbage and the influence of defoliation on aboveground phytomass production.

Plant-herbivore dynamics on rangelands depend on pasture productivity, changes in phytomass with time, and the vegetation's responses to defoliation (Caughley 1976; 1982; Noy-Meir 1975). Defoliation may influence the dynamic interaction between plant growth rates and phytomass, as well as change the proportions of green herbage, standing dead and fallen litter pools.

There is no definitive description or terminology for live and dead vegetation material in range ecosystems. Range ecologists have used different terms for vegetation components; e.g., above- and below ground phytomass, dead-shoot phytomass, recent dead, old-dead, mulch, litter, standing litter, ground litter, and standing dead (Odum 1960; Golley 1965; Tomanek 1969; Coupland 1979; Heitschmidt et al. 1982). For this study, green herbage refers to green photosynthesizing material of growing plants; standing dead refers to cured or dried plant material still attached to the standing plant; and fallen litter consists of detached undecayed plant residuum lying on the soil surface (Dyksterhuis and Schmutz 1947).

The timing, intensity, and frequency of defoliation interact in complex ways on production processes and herbage yield in rangeland ecosystems (McNaughton 1983; Oesterheld and McNaughton 1988; Heady and Child 1994; Zhang and Romo 1994). There are unique and important plant-animal interactions within grazed grasslands of the aspen boreal ecosystems. In particular, most of the tame pastures of Bromegrass-Bluegrass (*Bromus inermis-Poa pratensis*) are preferred by many free-ranging native ungulates and diversified ungulate livestock, such as Wapiti (*Cervus elaphus*) (Looman 1976; McCartney 1993). However, little information exists on the seasonal dynamics of available forage and the effects of alternative defoliation regimes on herbage growth which is needed to formulate improved

management decisions related to grazing and animal production. Therefore, in this study, we used an experimental design to investigate: (1) seasonal changes in the live and dead phytomass components of a *Bromus inermis-Poa pratensis* community; and (2) the effects of initial timing, height and frequency of clipping on accumulated herbage removal. The study reported herein was conducted to test the following hypotheses: (1) Amounts of herbage available for grazing change seasonally; and (2) Initial timing, height and frequency of clipping would affect accumulated herbage removal.

Materials and Methods

Study Site

Field research was conducted at the University of Alberta Ministik Wildlife Research Station (53° 18'N, 114° 35'W), located 48 km southeast of Edmonton, Alberta, on the Cooking Lake glacial moraine. Vegetation is classified as boreal aspen forest (Rowe 1972; Strong 1992), although homesteading in the early 1900s created characteristics more similar to those of the Aspen Parkland. Major vegetation types include Balsam Poplar (*Populus balsamifera*) and Trembling Aspen (*P. tremuloides*) forests, *Bromus inermis-Poa pratensis* grasslands and Threadleaf Sedge (*Carex filifolia*) wetlands. Seeded in the early 1950s, the grasslands are dominated by Smooth Brome (*Bromus inermis*) and Kentucky Bluegrass (*Poa pratensis*). Smooth Brome is a tall, leafy, rhizomatous, cool-season perennial that is long-lived and grows rapidly (Hardy Associates, Ltd. 1989). Kentucky Bluegrass is a short-statured, long-lived, cool-season perennial that spreads via extensive rhizomes. Dicotyledonous plants include White Clover (*Trifolium repens*) and Dandelion (*Taraxacum officinale*). Grasses typically initiate growth in late-April or early May following snow melt, with swards dominated by vegetative graminoids in mid-May. Grasses head in June with seed-ripe by mid-August. The dominant dicot, Dandelion, emerges in early-May, becomes the most visible dicot in early-June and persists to autumn. Following Dandelion, clovers reach their peak phytomass in July, and survive until the end of the frost-free period. Grasses senesce in late-September and October. The pastures used in this study were grazed by Rocky Mountain Wapiti (*Cervus elaphus*) at a stocking rate of approximately 2.0 AUM [animal unit months] ha^{-1} in the years prior to the study.

Average annual precipitation of the area varies from 400 to 450 mm with 334 mm falling during the growing season (April to September). Mean temperatures average -17.3°C and +17.4°C for January and July, respectively, with absolute temperatures ranging from –49 to +32 °C (Olson 1985).

Soils are mainly moderately well- to well-drained Luvisols. The upland Cooking Lake loam, which predominates in the region (Bowser et al. 1962), is a fairly well-drained Orthic Gray Luvisolic soil developed on glacial till of the Edmonton formation, underlying forested areas. The Uncas loam, an Orthic Dark Gray Luvisolic soil, also developed from glacial till, is found on less densely forested areas. Sandy loams are also present on the area, though in low proportions.

Experimental Procedure

A 20 × 60-m exclosure was established in April 1997 to protect plots from grazing. To ascertain the vegetation growth pattern for the area, thirty plots, each 40 × 40 cm, were permanently marked within the site. Clip samples were obtained at monthly intervals from five randomly selected plots from April to September 1997. All phytomass within each plot was harvested to ground level and litter removed to mineral soil. Sampling was subsequently repeated on the same plots on the same dates in 1998. This eliminated the potential effects of age differences between sites. All harvested material was hand sorted into components of live green plant material, dry plant material (standing dead), and fallen litter, dried at 60°C, and weighed. Measurements were not made from October to March because snow cover and freezing temperatures limited field activities.

To describe the plant community in the study area, five 10-m line transects were marked across the exclosure at five regular intervals in 1998. A 30 × 30 cm quadrat was used to systematically sample along each transect in midsummer (n = 20 quadrats). Within each quadrat, all plant species were identified and their percent cover estimated (Daubenmire 1959).

To establish the relationship between plant growth and herbage removed, clipping treatments with three initiation dates, three heights and three frequencies (e.g., intervals) were replicated six times in a completely randomized design over the two years (1997 and 1998). All plots were 40 × 40 cm permanently marked, with a 10-cm clipped buffer maintained on all sides. Levels of the independent factors were: date of initial clipping (20 May, 22 June, and 22 July); heavy, moderate, and light intensities (clipping heights of 2.5, 7.5, and 15 cm from ground level); clipping frequency (three, six and nine week intervals after initial defoliation); and time (first and second years growth). Sub-plots of 20 × 20 cm were clipped on each plot at ground level at the end of September in each year to determine residual (season-end) phytomass. Aboveground phytomass was calculated from the sum of plant material collected at each clipping date plus residual phytomass. Treatments were imposed on the same plots each year. All samples were oven-dried at 60°C and weighed. Mean percent soil water content (from five readings) of the 0 to 30 cm soil increment at the study site was measured biweekly using gravimetric (mass) method (ASTM 1980). Soil sampling sites were chosen randomly from the area between clip plots.

TABLE 1. Monthly precipitation, soil water and average temperatures for Ministik Wildlife Research Station, Alberta, during the growing seasons of 1997 and 1998.

	Precipitation (mm)							Air Temperature (°C)		
Year	April	May	June	July	Aug.	Sept.	Total	Max.	Min.	Daily Average
1997	38	69	149	28	52	84	420	19	7	13
1998	34	38	111	89	21	50	343	21	9	15
1961-1990	10	40	77	89	78	40	334	18.6	7.4	13
				Soil water (g/100g)						
1997	15	19	28	22	17	16				
1998	13	16	22	19	12	13				

Note: Max = average maximum daily temperature, Min = average minimum daily temperature, Daily = average daily temperature.

Statistical Analyses

Comparisons of spring, summer and fall phytomass of green herbage, standing dead and fallen litter herbage components were made. The effects of date of initial clipping, clipping height, clipping frequency and year were analyzed with a factorial analysis of variance using PROC GLM of SAS (SAS Institute, Inc. 1989). Preliminary tests prior to the ANOVA indicated no deviation from normality. Post-hoc mean comparisons were done on all significant treatment means and their interactions using Tukey's method ($P \leq 0.05$).

Results

Weather and soil water

Total annual precipitation at the Ministik area for 1997 and 1998 was 494 and 429 mm, compared to a long-term average of 425 mm. Growing season precipitation (April to September) in 1997 was 26% above the long-term average (Table 1). Growing season precipitation for 1998 was slightly above average. Average air temperatures experienced during the growing season in 1997 were normal, but exceeded the average in 1998 (Table 1). Soil water content varied during the entire growing season for both years. Soil water content in the top 30 cm of soil increased from approximately 14% of soil weight in April to a peak of 26% in June (Table 1). Overall, weather conditions at Ministik during the growing season of 1997 were more favorable for herbage production than in 1998.

Plant Composition and Seasonal Changes of Herbage Phytomass

Plant species composition data showed a community dominated by Kentucky Bluegrass and Smooth Brome (Table 2). The three phytomass pools of green herbage, standing dead and fallen litter generally increased from spring to summer and subsequently decreased from summer to fall (Table 3). In 1997, green herbage increased by 107% from spring to summer and decreased by 39% from summer to fall. The same trend was observed in 1998 with a 105% increase and 26% decrease, respectively. Standing dead and litter followed the same trends, peaking in midsummer during both years, although summer and fall pools of standing dead and litter were generally did not differ significantly from one another. Seasonal accumulation of herbage phytomass was generally greater in 1997 than 1998,

TABLE 2. Composition (canopy cover) of major species in the *Bromus inermis–Poa pratensis* community at Ministik Wildlife Research Station, Alberta.

Species	Composition (%)
Grasses and Sedges	
Bromus inermis	41.3
Phleum pratense	5.8
Poa pratensis	22.1
Carex filifolia	4.8
Other grasses	2.4
Forbs	
Achillea millefolium	1.5
Aster sagittifolius	4.9
Cirsium arvense	1.9
Lathyrus sativus	2.2
Taraxacum officinale	8.8
Trifolium repense	3.1
Other forbs	1.2

TABLE 3. Seasonal changes of herbage phytomass (g m^{-2}) components on the *Bromus inermis-Poa pratensis* community at Ministik Wildlife Research Station, Alberta, in 1997 and 1998 (n = 5).

Sampling period interval	Green herbage	Standing dead	Fallen litter
1997			
Spring (15 April–3 June)	96 b[1]	77 c	22 b
Summer (4 June–31 July)	208 a	135 a	44 a
Fall (1 August–30 September)	127 b	113 b	35 a
SEM	11	8	6
1998			
Spring (15 April–3 June)	84 c	54 b	17 b
Summer (4 June–31 July)	178 a	90 a	45 a
Fall (1 August–30 September)	121 b	74 a	38 a
SEM	13	9	7

[1]Within columns in a given year, means with different letters are significantly different ($P \leq 0.05$).

likely due to the higher precipitation in 1997. Weathering losses of green herbage, standing dead and fallen litter over winter (i.e., between fall 1997 and spring 1998) expressed as a proportion of the fall 1997 estimate were 34, 52 and 51%, respectively (Table 3). Dry matter losses of total herbage (all 3 pools) over winter were 58% of 1997 summer green phytomass.

Defoliation Effects on Aboveground Productivity

Clipping date, height and frequency all had significant effects on accumulated aboveground herbage removal between years (Table 4) and within years (data not shown). The effect of year on aboveground forage removal was independent of clipping height and frequency. Clipping date affected forage yield the most, with yield values differing significantly among all three dates investigated but peaking with May clipping (Table 5). Herbage yield following July clipping was less than half that of May. Heavy and moderate clipping intensities increased herbage removal relative to the light intensity clipping (Table 5). Raising the clipping height from 7.5 to 15 cm reduced herbage yield by 27%. The greatest accumulated herbage yield was found with longer regrowth periods (e.g., six or nine weeks rest) (Table 5). The significant interaction between clipping date and clipping frequency (Table 4) was attributed to the increased positive effect of longer recovery times following May clipping, as well as a contrasting reduction in forage yield with longer recovery times following later initial dates of defoliation.

TABLE 4. Analysis of Variance (F-values) of total accumulated dry matter yield from defoliation treatments at Ministik Wildlife Research Station in Alberta, 1997 and 1998.

Source of Variation	df	Yield (g m^{-2})
Year (Y)	1	4.50 *
Defoliation Date (D)	2	65.22 **
Defoliation Height (H)	2	20.75 **
Defoliation Frequency (F)	2	31.63 **
YxD	2	4.41 *
YxH	2	2.98
YxF	2	2.60
DxH	4	17.05 **
HxF	4	1.49
YxDxH	4	1.65
YxDxF	4	0.82
YxHxF	4	0.56
DxHxF	8	1.34
YxDxHxF	8	0.89

* $P \leq 0.05$, ** $P \leq 0.01$.

TABLE 5. Effects of defoliation date, height, and frequency on total accumulated dry matter yield (SD in parenthesis) of *Bromus inermis-Poa pratensis* pasture in Alberta.

Treatments	df	Yield (g m^{-2})	
Defoliation Date (D)	2		
May 20		147.97	(12.37)a
June 22		95.27	(6.07)b
July 22		59.15	(4.07)c
Defoliation Height	2		
2.5 cm		104.22	(10.61)a
7.5 cm		113.06	(10.04)a
15 cm		84.47	(7.75)b
Defoliation Frequency	2		
3 weeks		64.33	(3.11)b
6 weeks		119.31	(6.54)a
9 weeks		118.75	(5.56)a

Within treatments, means with different letters are significantly ($P \leq 0.05$) different.

Discussion

Seasonal herbage production on pastures is influenced by plant community type, local growing conditions, and disturbance regime. Areas with a history of grazing are generally characterized by reduced litter (Willms et al. 1986), decreased annual production, increased losses of herbage over winter, and delayed spring growth (Willms et al. 1996). The maximum seasonal phytomass of each herbage component documented in summer coincided with wet soil conditions. In this study, there were over-winter losses of total herbage, standing dead and fallen litter. These losses are of economic importance in this area because grazing animals such as Wapiti forage through snow during winter months, and hence it is necessary to maintain a high proportion of herbage on winter ranges to ensure adequate grazing opportunities. Low spring yield in the *Bromus inermis-Poa pratensis* community was likely due to dry soil conditions or slow growth of plants. High herbage yield in summer was dependent on precipitation during the growing season. Shallow-rooted, rhizomatous species (like those dominant in this community) are most productive with frequent showers since moisture conservation tends to be inefficient with reduced litter (Willms et al. 1996). Clipping or grazing can also change the distribution of roots in the soil by reducing the rooting depth and packing more roots in the soil surface (Willms 1991; Smoliak et al. 1972). Herbage yield response to precipitation late in the growing season also tends to be low because many species have completed their growth cycle and the onset of cooler temperatures may impede growth.

Numerous studies have demonstrated the effects of fertilizer, legumes, and defoliation on grasslands in western Canada (Johnston et al. 1971; Smoliak et al. 1972; Ukrainetz et al. 1988; Pearen and Baron 1996; McCartney et al. 1999). Most of these studies have taken place on nutrient rich soils in the Black Chernozemic soil zone, rather than the less fertile Gray Luvisolic soils of the Boreal Mixedwood where many commercial game ranching enterprises are located (McCartney et al. 1999). By conducting studies on the latter, the effects of defoliation on pasture growth and productivity can be established for an area representative of a large region of central Alberta impor-

tant for commercial livestock production, diversified ungulate livestock and free-ranging native ungulates.

In addition to the within-year seasonal variation of herbage yield and overwinter losses in phytomass, the influence of initial timing, height and frequency of clipping affected phytomass yield both within and between years in this boreal environment. These variable responses are attributed to differences in environmental conditions between years and the cumulative effects of defoliation in current and preceding years (Zhang and Romo 1994).

The greatest herbage harvested was associated with clipping initiated in May, and peaked with at least six weeks rest (regrowth). Increases in herbage yield should be more pronounced during the early active growth period of plants than later on when growth is constrained by seed-head production. This trend is particularly prevalent because the dominant grasses are all C3 species, which typically produce maximum growth by July (Zhang and Romo 1994). This pattern is also indicative of species well adapted to withstand herbivory (e.g., rhizomatous species). The decline in herbage yield associated with initial clipping in July may be due to lower soil moisture availability after mid-summer. In addition, higher temperatures in late-summer can depress forage production of cool-season species (Cooper 1979; DePeters and Kesler 1985; Mason and Lachance 1983). These results agree with other studies (e.g., Cooper 1956; DePeters and Kesley 1985; Dovel 1996), wherein pasture regrowth from defoliation in spring represented nearly half of the total growing season yield.

Moderate defoliation at all times appeared to increase herbage yield in this study. Similar results have been obtained in other studies (Robinson et al. 1952; Cooper 1956). Studies examining the effect of clipping height on yield of individual grass species suggest between 2.5 and 5 cm as an optimal clipping height (e.g., Reid 1966). Intensity of defoliation directly controls the herbage remaining for optimal regrowth (Heady and Child 1994). In a study adjacent to our research site that examined remaining herbage (stubble) in response to defoliation heights, Okello (1996) recorded season-long herbage stubble of 90, 120, and 170 g m^{-2} from 2.5, 7.5, and 15 cm defoliation heights. Remaining herbage values for these pastures at the 7.5-cm clipping height exceeded the recommended level of 100 g m^{-2} for optimizing forage production in many pastures (Smethen 1990). Thus, a relatively intense defoliation height between 2.5 and 7.5 cm may be needed to optimize forage production on these particular pastures. We agree, however, with Dovel's (1996) assertion that factors other than forage yield, such as type of vegetation, stand vigor and animal performance must also be considered in determining the optimum defoliation intensity (e.g., height).

Frequent clipping has often resulted in reduced yield compared to less frequent harvests (Ethredge et al. 1973; Owensby et al. 1974). In this study, the greatest yield was obtained from clipping no less than six weeks after initial defoliation. Rotational grazing is an important option for increasing pasture production in the Aspen Parkland (see McCartney 1999). It is obvious from these data that pastures should be rested for six weeks during rotational grazing if season-long yields are to be maintained.

The interaction between initial defoliation date and clipping frequency may be related to the phenology of plants within the study area. Plants tend to grow rapidly in the early part of the growing season, with defoliation causing photosynthates to be translocated to defoliated sites for tissue repair rather than growth (McNaughton 1979). Changes in below ground phytomass may also parallel aboveground phytomass, with root development requiring re-initiation (e.g., Johnston et al. 1971). This trend changes, however, as plants mature: growth rates decline and products of photosynthesis are preferentially utilized for reproduction (Harper 1977; Krebs 1985). Also, compensation in the defoliated plants along the growing cycle depends on the length of time available for recovery (Hilbert et al. 1981). Hence, it appears from these results that longer recovery times are more beneficial during early defoliation and vice versa.

Pasture response to defoliation varied with the growing cycle of major plants and corresponded with precipitation and soil moisture conditions. Williamson et al. (1989) stressed the need to understand the interactive role of soil water content and defoliation treatments as essential to understanding the relationship of grazing and herbage production. Maximum herbage production under defoliation may occur under certain hydrologic conditions, such as when water remains non-limiting despite grazing induced changes in root phytomass. Defoliation may also result in less water uptake and increased soil water availability later in the growing season, subsequently increasing productivity. In contrast, the lack of defoliation early in the growing season may result in early maturation of the herbage and less efficient use of any remaining soil moisture in mid- to late summer.

Conclusions

Maximum summer yield, rapid loss of green herbage late in the growing season, and dry matter losses in the standing dead and fallen litter pools over winter characterized the seasonal changes in herbage phytomass on this Aspen Boreal grassland. The amount of herbage harvested was affected by initial clipping date, clipping height and frequency of clipping. Pasture response to clipping varied with the growth cycle of major plants and also corresponded with the soil water conditions of the area. The interaction between clipping date and frequency demonstrates the importance of temporal rest and resource allocation for the sustained productivity of herbage plants.

The defoliation intensities adopted in this study are consistent with field observations of livestock and wildlife grazing. However, we acknowledge that clipping is not equivalent to grazing as it excludes trampling impacts, shredding and the behavioral role of the grazing animal as an ecosystem regulator, selectively facilitating energy flow and the local cycling, redistribution and transformation of nutrients on the landscape. Hence, work is needed with actual grazing systems under field studies to further validate these findings. The value of our study is to show wildlife and other resource managers the need for controlled defoliation in pasture-based systems utilized by diversified ruminant livestock and free-ranging native ungulates to ensure efficient and sustainable use of these habitats.

Acknowledgments

We acknowledge the financial support of Alberta Agricultural Research Institute. We would like to thank Lisa Yadenuk, Paul Hansen and Dave HayDuk for competent fieldwork. The authors wish to thank Drs. Rod Heitschmidt, Anne Naeth and David Chanasyk for their helpful comments during manuscript preparation.

Literature Cited

American Society for Testing Materials. 1980. Standard method for laboratory determination of water (moisture) content of soil, rock and soil aggregate mixtures. ANSI/ASTM D2216-8 Annual Book of ASTM standards, Part 19. Philadelphia. 276 pages.

Baron, V. S., and **R. P. Knowles.** 1984. Use and improvement of meadow brome as a pasture species for Western Canada. Proceedings of the 2nd intermountain meadow symposium. Special series, number 34, Colorado State University and University of Wyoming Agricultural Experimental Stations.

Bork, E. W., R. J. Hudson, and **A. W. Bailey**. 1997. Populus forest characterization in Elk Island National Park relative to herbivory, prescribed fire, and topography. Canadian Journal of Botany 75: 1518-1526.

Bowser, W. E., A. A. Kjearsgaard, T. W. Peters, and **R. E. Wells.** 1962. Soil survey of Edmonton Sheet (83-H). Alberta Soil Survey Report (21). Canada Department of Agriculture.

Caughley, G. 1976. Plant-herbivore systems. Pages 99-113 *in* Theoretical ecology: principles and applications. *Edited by* R. M. May. W. B. Saunders, Philadelphia.

Caughley, G. 1982. Vegetation and the dynamics of modeled grazing systems. Oecologia 54: 309-312.

Cooper, C. S. 1956. The effect of time and height of cutting on the yield, crude protein content, and vegetative composition of native flood meadow in Eastern Oregon. Agronomy Journal 48: 257-258.

Cooper, C. S. 1979. Yields of irrigated grass and legume pasture mixtures in the Northern Rocky Mountain area. Agronomy Journal 71: 885-888.

Coupland, R. T. 1979. Grassland ecosystems of the world: analysis of grasslands and their uses. Cambridge University Press. Cambridge, England. IBP 18. 401 pages.

Daubenmire, R. F. 1959. Canopy coverage method of vegetation analysis. Northwest Science 33: 43-64.

DePeters, E. D., and **E. M. Kesler.** 1985. Yields and nutritive value of cuttings and permanent pasture harvested as dry hay forage. Journal of Dairy Science 68: 996-999.

Dovel, R. L. 1996. Cutting height effects on wetland meadow forage yield and quality. Journal of Range Management 49: 151-156.

Dyksterhuis, E. J., and **L. M. Schmutz.** 1947. Natural mulches or litter of grassland with kinds and amounts on a southern prairie. Ecology 28: 163-179.

Ethredge, J., E. R. Beaty, and **M. L. Lawrence.** 1973. Effects of clipping height, clipping frequency and rates of nitrogen on yield and energy content of coastal bermudagrass. Agronomy Journal 65: 717-719.

Golley, F. B. 1965. Structure and function of an old-field brome-sedge community. Ecological Monographs 35: 113-137.

Hardy Associates, Ltd. 1989. Manual of plant species suitability for reclamation in Alberta (2nd edition), Alberta Land Conservation and Reclamation Council Report RRTAC 89-4. 436 pages.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York. 892 pages.

Heady, H. F., and **R. D. Child.** 1994. Range ecology and management. Westview Press, Boulder, Colorado. 519 pages.

Heitschmidt, R. K., D. I. Price, R. A. Gordon, and **J. R. Frasure.** 1982. Short duration grazing at the Texas Experimental Ranch: Effects on aboveground net primary production and seasonal growth dynamics. Journal of Range Management 35: 367-372.

Hilbert, D. W., D. M. Swift, J. K. Detling, and **M. I. Dyer.** 1981. Relative growth rates and the grazing optimization hypothesis. Oecologia (Berlin) 51: 14-18.

Johnston, A., J. F. Dormaar, and **S. Smoliak.** 1971. Long-term grazing effects on fecue grassland soils. Journal of Range Management 24: 185-188.

Krebs, C. J. 1985. Ecology: the experimental analysis of distribution and abundance. 3rd edition. Harper and Row Publishers, New York. 892 pages.

Looman, J. 1976. Productivity of permanent bromegrass pastures in the Parklands of the Prairie Provinces. Canadian Journal of Plant Science 56: 829-835.

Mason, W., and **L. Lachance.** 1983. Effects of initial harvest date on dry matter yield, in vitro dry matter digestibility, and protein in timothy, tall fescue, reed canary grass, and Kentucky bluegrass. Canadian Journal of Plant Science 63: 675-685.

McCartney, D. H. 1993. History of grazing research in the Aspen Parkland. Canadian Journal of Animal Science 73: 749-763.

McCartney, D. H., J. Waddington, and **L. P. Lefkovitch.** 1999. Animal and plant response on renovated pastures in western Canada. Journal of Range Management 52: 19-26.

McNaughton, S. J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist 113: 691-703.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40: 329-336.

Noy-Meir, I. 1975. Stability of grazing systems: an application of predator-prey graphs. Journal of Ecology 63: 459-481.

Odum, E. P. 1960. Organic production and turnover in old field succession. Ecology 41: 34-49.

Oesterheld, M., and **S. J. McNaughton.** 1988. Intraspecific variation in the response of *Themeda triandra* to defolia-

tion: the effect of time of recovery and growth rates on compensatory growth. Oecologia 77: 181-186.

Okello, M. M. 1996. Dynamics of ungulate – plant grazing systems. Ph.D. thesis, University of Alberta, Edmonton. 82 pages.

Olson, R. 1985. The climate of Edmonton. Climatological studies (37), The Climate of the Canadian Cities (2), Environment Canada, Ottawa, Canada.

Owensby, C. E., J. R. Rains, and **J. D. McKendrick.** 1974. Effects of one year of intensive clipping on big bluestem. Journal of Range Management 27: 341-343.

Pearen, J. R., and **V. S. Baron.** 1996. Productivity, and composition of smooth and meadow Bromegrass mixtures with alfalfa under frequent cutting management. Canadian Journal of Plant Science 76: 763-771.

Reid, D. 1966. Studies on cutting management of grass clover swards. 4. The effect of close and lax cutting on the yield of herbage from swards cut at different frequencies. Journal of Agricultural Science 66: 101-106.

Robinson, R. R., V. G. Sprague, and **A. G. Lueck.** 1952. The effect of irrigation, nitrogen fertilization, and clipping treatments on persistence of clover and on total and seasonal distribution of yields in a Kentucky bluegrass sod. Agronomy Journal 44: 239-244.

Rowe, J. S. 1972. Forest regions of Canada. Department of Environment, Canada Forest Service Publication (1300). 172 pages.

SAS Institute, Inc. 1989. SAS/STAT user's guide: Version 6, 4th edition. Volume 2. SAS Institute Inc. Cary, North Carolina.

Smethen, M. L. 1990. Pasture management. Pages 197-240 *in* Pastures, their ecology and management. *Edited by* R. H. M. Langer. Oxford University Press, Oxford.

Smoliak, S., J. F. Dormaa, and **A. Johnston.** 1972. Long-term grazing effects on *Stipa-Bouteloua* Prairie soils. Journal of Range Mangement 25: 246-250.

Strong, W. L. 1992. Ecoregions and ecodistricts of Alberta. Volume 1. Publication of the Alberta Forestry, Lands, and Wildlife, Edmonton, Alberta.

Telfer, E. S., and **G. W. Scotter.** 1975. Potential for game ranching in boreal aspen forest regions of western Canada. Journal of Range Management 28: 172-180.

Tomanek, G. W. 1969. Dynamics of mulch layer in grassland ecosystems. Pages 225-240 *in* The grassland ecosystem and preliminary synthesis. *Edited by* R. L. Dix and R. G. Beidleman. IBP Range Science Department Science Series (2).

Ukrainetz, H., C. A. Campell, R. P. Zentner, and **M. Monreal.** 1988. Response of bromegrass to N-fertilizer, P-fertilizer and S-fertilizer on a gray Luvisolic soil in northwestern Saskatchewan. Canadian Journal of Plant Science 68: 687-703.

Williamson, S. C., J. K. Detling, J. L. Dodd, and **M. I. Dyer.** 1989. Experimental evaluation of the grazing optimization hypothesis. Journal of Range Management 42: 149-152.

Willms, W. D. 1991. Cutting frequency and cutting height effects on rough fescue and Parry oatgrass yields. Journal of Range Management 39: 536-540.

Willms, W.D., S. Smoliak, and **A. W. Bailey.** 1986. Herbage production following litter removal on Alberta native grasslands. Journal of Range Management 39: 536-540.

Willms, W. D., B. W. Adams, and **J. F. Dormaar.** 1996. Seasonal changes of herbage biomass on the fescue prairie. Journal of Range Management 49: 100-104.

Zhang, J., and **J. T. Romo.** 1994. Defoliation of a northern wheatgrass community: Above- and belowground phytomass productivity. Journal of Range Management 47: 279-284.

Received 6 March 2001
Accepted 12 November 2003

Patterns of Nestling Feeding in Harris's Sparrows, *Zonotrichia querula* and White-crowned Sparrows, *Z. leucophrys,* in the Northwest Territories, Canada

CHRISTOPHER J. NORMENT[1]

Museum of Natural History and Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045 USA
[1]Current address: Department of Environmental Science and Biology, SUNY College at Brockport, Brockport, New York 14420; e-mail: cnorment@brockport.edu

Norment, Christopher J. 2003. Patterns of nestling feeding in Harris's Sparrows, *Zonotrichia querula,* and White-crowned Sparrows, *Z. leucophrys,* in the Northwest Territories, Canada. Canadian-Field Naturalist 117(2): 203–208.

Patterns of nestling feeding by males and females were compared in sympatric populations of Harris's Sparrows (*Zonotrichia querula*) and Gambel's White-crowned Sparrows (*Z. leucophrys gambelii*) in the Northwest Territories, Canada. In both species, only the female brooded young. Total feeding rate (both parents), and male and female feeding rates, increased with nestling age in both species; total feeding rates did not differ significantly between species. Nestlings of both species were fed most frequently by females during the early part of the nestling period (day 0-5), and feeding rates did not approach parity until nestlings were 6-8 d old. Patterns of nestling feeding, including initially low male provisioning, in Harris's Sparrows and White-crowned Sparrows at my low arctic study site were similar to those in other populations of *Zonotrichia*. Low levels of male nestling care, relative to females, appears to be relatively uncommon among socially monogamous passerines. Reduced male care may be adaptive in temperate environments, as it would allow males to pursue other mating opportunities. However, reasons for persistence of the trait in the low arctic, where breeding is highly synchronous, remain unclear.

Key Words: Harris's Sparrow, *Zonotrichia querula*, White-crowned Sparrow, *Zonotrichia leucophrys*, breeding biology, nestling care, Northwest Territories.

Nestling care is an important component of reproduction in passerine birds and requires high parental investment (PI) (Ricklefs 1974; Walsberg 1983). Unequal male versus female PI during the nestling phase of the breeding cycle occurs in many passerines (e.g., Hegner and Wingfield 1987; Yasukawa et al. 1990; Haggerty 1992). These asymmetries may arise from conflict between the sexes (Gowaty 1996a, b) and may be linked to the evolution of avian mating systems (Emlen and Oring 1977). Because of the assumed "cost of reproduction," high levels of PI may reduce adult survival probabilities, and select for reduced clutch size (Williams 1966).

In 1989-1991, I studied nestling care in sympatric Harris's Sparrows (*Zonotrichia querula*) and Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) in the Northwest Territories (NWT), Canada. Here I compare effects of nestling age on parental feeding rates and the relative contribution of males and females to nestling feeding in these species. Nestling care has been studied previously in White-crowned Sparrows; both sexes feed the young, but only females brood nestlings (Chilton et al. 1995). The same pattern occurs in Harris's Sparrows (Norment and Shackelton 1993), although nestling care in the species had not been investigated in detail prior to this study. I used a comparative approach to investigate *Zonotrichia* nestling care because there are relatively few such studies in sympatric passerine populations.

Study Area and Methods

I conducted the study at Warden's Grove (WG), Thelon Wildlife Sanctuary, Northwest Territories (63° 41'N, 104°26'W), during the summers of 1989-1991. The low arctic study area contains a mosaic of isolated spruce (*Picea* spp.) stands and extensive tundra vegetation.

Tree "islands" are surrounded by shrubby Dwarf Birch (*Betula glandulosa*), willow (*Salix* spp.), and Green Alder (*Alnus crispa*) 0.3-1.5 m tall, which provide nesting habitat for *Zonotrichia*. The study area lies near the border between the arctic and boreal climatic regions (Hare and Thomas 1974), with cold winters and short, cool summers. In 1989-1991, mean ambient temperatures at WG ranged between 7.5 and 9.7°C in June and 12.5 and 16°C in July. Although the summers of 1989-1991 were relatively mild, violent storms may occur after breeding *Zonotrichia* arrive at WG (Norment 1985, 1992).

Nestling care was quantified by observing nests with 8× binoculars or 25× spotting scope from concealed locations or distances > 25 m, so as not to disturb attending birds. Nests of color-banded parents of known sex were observed for 1-h periods distributed throughout daily activity periods. Nests with young *Zonotrichia* were observed from day 0 to day 9 of nestling development, close to the average age of fledging for these species at WG (Norment 1992). Only nests observed on > 5 d, with nestlings of known

age with both parents present, and with broods in which nestling number remained constant, were used in analyses. Observation time was 78 h for Harris's Sparrow broods (n = 9 different broods; 3 broods with 3 nestlings, 4 broods with 4 nestlings, and 2 broods with 5 nestlings), and 36 h for White-crowned Sparrow broods (n = 4 different broods: 2 broods with 4 nestlings and 2 broods with 5 nestlings). White-crowned Sparrow sample size was limited by its breeding density, which was 33% that of Harris's Sparrows (Norment 1992). Number of broods observed for each species was almost constant across years (Harris's Sparrow: 3 broods in each year; White-crowned Sparrow: 1 brood each in 1989 and 1991, 2 broods in 1990). During the study, sex of the attendant bird(s) and their activities (feeding young or brooding) were recorded. Because adult *Zonotrichia* feeding nestlings usually perch in conspicuous locations before visiting the nest (personal observation), sex of attendant banded birds could be determined.

Male, female, and combined parental feeding rates were calculated for each nest during each 1-h observation period. I used linear regression to examine nestling age effects on nestling feeding rates using mean values for each age (0-9 d), based on all nests observed. I examined interspecific differences in nestling feeding rates by using the general linear model to do a two-factor ANOVA with feeding rate as the response variable, and nestling age (days 0-9) and species as factors. I also used the general linear model for an intersex comparison of Harris's Sparrow nestling feeding rates, with nestling age (days 0-9) and sex as factors. In these analyses, cells contained number of feedings/h for individual nests (n = 9 nests). I also used the general linear model to test for an interaction effect between Harris's Sparrow brood size and sex, based upon mean feeding rates for each nest. When sample sizes varied across days or species, I used the square-root transformation to reduce inequality among variances (Zar 1999). If a significant interaction term was present for any two-factor ANOVA, then a single-factor ANOVA was used to compare means of a factor separately at each level of the second factor (Underwood 1997). Finally, I used the Wilcoxon signed-ranks test (Sokal and Rohlf 1981) for an intersex comparison of Harris's Sparrow nestling feeding rates across the range of nestling ages; for this I compared mean values for each member of each pair for early (day 0-2), middle (day 3-5) and late (day 6-8) stages of nestling care. Significance level for all analyses was 0.05; $x \pm$ SD are given throughout, unless otherwise indicated.

TABLE 1. Two-factor ANOVA for effects of sex and nestling age on male and female feeding rates for Harris's Sparrows.

Source	*df*	SS	MS	*F*	*P*
Sex	1	12.7965	11.57774	57.97	0.000
Nestling age	9	20.0790	2.2310	11.17	0.000
Sex* nestling age	9	7.3311	0.8146	4.08	0.000
Error	134	26.7621	0.1997		
Total	153	66.9688			

Results

During > 114 h of nest observations, only female Harris's Sparrows and White-crowned Sparrows brooded nestlings. Males of both species fed nestlings, but attendant males never stayed > 2 min at a nest. Combined feeding rate (both parents) increased with nestling age in Harris's Sparrows (r = 0.954, P < 0.001) and White-crowned Sparrows (r = 0.926, P = 0.006) (Figure 1). Harris's Sparrows tended to feed day 0 and day 3 nestlings more frequently than did White-crowned Sparrows, but feeding rates for Harris's Sparrows were lower than for White-crowned Sparrows for day 5-9 nestlings (Figure 1). Across the range of nestling ages, there was no significant difference between species in combined feeding rates (Two-factor ANOVA; df = 1, F = 0.54, P = 0.465).

Harris's Sparrow and White-crowned Sparrow nestlings were fed most often by females during early stages of the nestling period; percentage of male feeding trips attained maximum values of ca. 47% of total feedings when nestlings were between day 6 and 9 (Figure 1). Male White-crowned Sparrows generally fed nestlings on day 0, whereas all banded male Harris's Sparrows known to be > 1 yr began feeding nestlings by day 1. However, a few Harris's Sparrow males appeared reluctant to feed nestlings < 3 d. At several nests, females returning from foraging trips perched within several m of the nest and gave a long series of "*chink*" calls. These were repeated until the male fed the young, at which time the female ceased calling and visited the nest. This behavior was not seen in White-crowned Sparrows and ceased after males began regular feedings.

Total feedings were higher for female than for male Harris's Sparrows (62.5%, n = 748) and White-crowned Sparrows (60.2%, n = 304). Male feeding rates increased with nestling age for Harris's Sparrows (r = 0.965, P < 0.001) and White-crowned Sparrows (r = 0.951, P < 0.001) (Figure 1). Female feeding rates also increased with nestling age for Harris's Sparrows (r = 0.780, P = 0.005) and White-crowned Sparrows (r = 0.878, P <0.001) (Figure 1). Because there was a significant interaction term between sex and age (Two-factor ANOVA; Table 1), I used single-factor ANOVAs to compare male and female feeding rates at each nestling age (see Methods). Average feeding rates for Harris's Sparrow broods were significantly greater for females than for males from day 0 through day 4, but not for day 5 through day 9 (Figure 1). The Wilcoxon signed-ranks test also indicated that female Harris's Sparrows fed nestlings significantly more often than males through

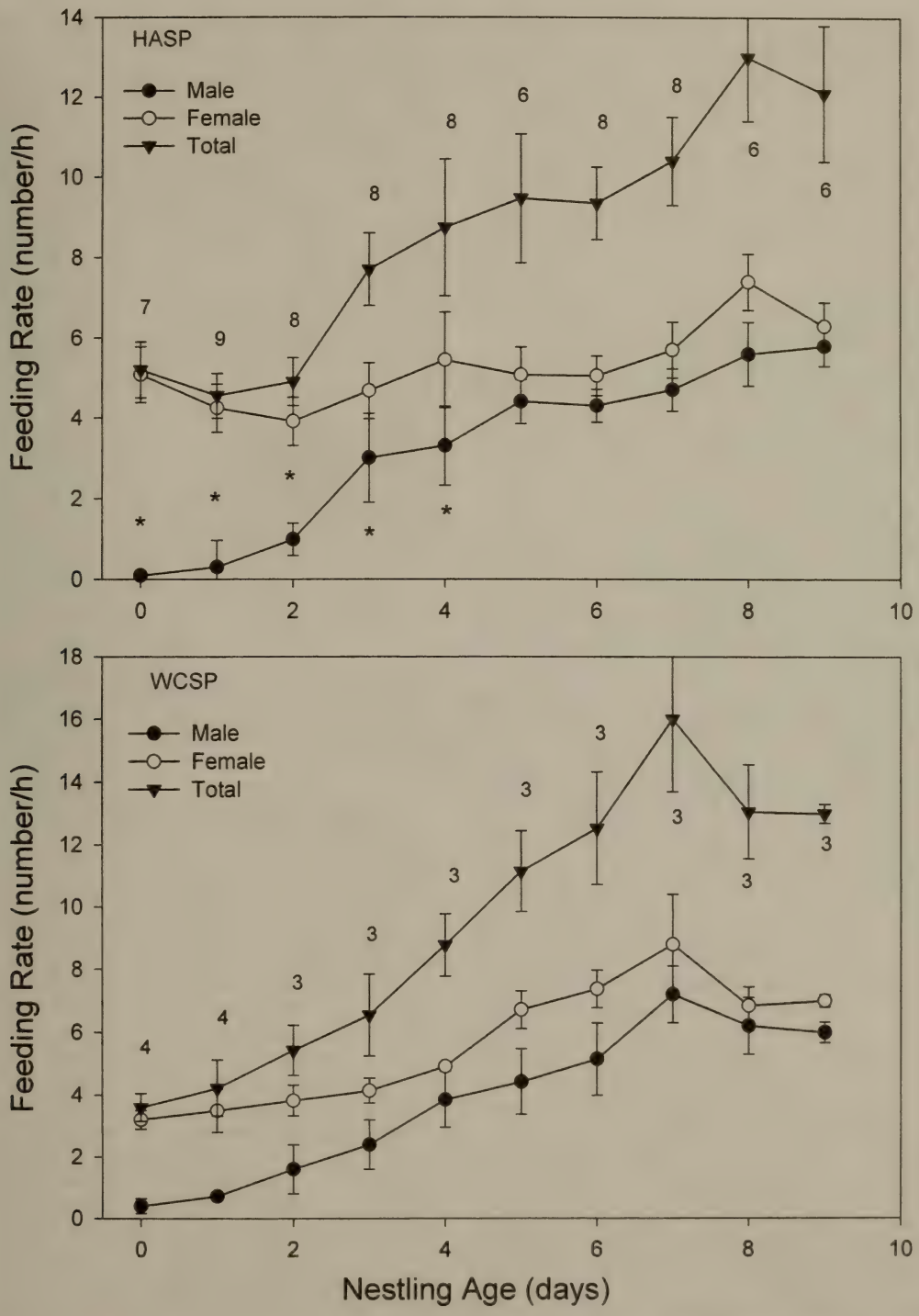


FIGURE 1. Mean feedings/h for both parents (Total), males, and females plotted against nestling age for Harris's Sparrows (HASP, top) and White-crowned Sparrows (WCSP, bottom) at Warden's Grove, 1989-1991. Error bars indicate ± 1 SE. Sample sizes (observation periods) given for each nestling age;* on the HASP graph indicate significant differences ($P < 0.05$) for single-factor ANOVAs comparing male and female feeding rates for broods of a single age (see Methods).

the early and middle stages of nestling care, but not during the late stage (Table 2, $P < 0.05$). Patterns were similar in White-crowned Sparrows, but sample sizes were too small for the Wilcoxon test (Table 2). Brood size significantly affected Harris's Sparrow feeding rates, with lower rates in smaller broods ($P = 0.003$), although male feeding rates were smaller than female feeding rates for all brood sizes ($P < 0.001$) and there was no significant interaction between sex and brood size (Two-factor ANOVA; Table 3).

Discussion

Patterns of nestling care in Harris's Sparrows and White-crowned Sparrows at WG were similar to those observed elsewhere in *Zonotrichia*. Both sexes feed nestlings, but only the female broods young, in White-crowned Sparrows (Chilton et al. 1995), Rufous-collared Sparrows (*Z. capensis*; Miller and Miller 1968) and Golden-crowned Sparrows (*Z. atricapilla*; Norment et al. 1998). In White-throated Sparrows (*Z. albicollis*) brooding is primarily by females, although males occasionally brood (Falls and Kopachena 1994). Male *Zonotrichia* usually feed nestlings less than females, with the proportion of male feedings remaining low during the first few days after nestlings hatch (DeWolfe 1968; Hendricks 1987a; Knapton and Falls 1983; Morton 2002).

Feeding nestlings, particularly as they approach fledging, is energetically expensive for arctic passerines (Custer et al. 1986). In Harris's Sparrows and White-crowned Sparrows, combined parental feeding rates and male feeding rates increased with nestling age; female feeding rates also increased, but less steeply than male rates. Both the relative contribution of males to feeding nestlings < 3d, and their overall feeding rates, were lower than for females of both species. These differences probably were not due to brood size effects. Brood size affects patterns of male and female parental investment in some socially monogamous passerines (Johnson and Best 1982; Hegner and Wingfield 1987; Westneat 1988; Carey 1990). However, I had equal numbers of White-crowned Sparrow broods of 4 and 5, and almost equal numbers of Harris's Sparrow broods of 3, 4 and 5, and the lack of an interaction effect between sex and brood size in the two-factor ANOVA (Table 3) suggests that brood size did not affect observed differences in male and female feeding rates in my study.

In four of the five *Zonotrichia* species, nestling feeding develops more slowly in males than in females, and males feed nestlings less frequently than females (Miller and Miller 1968; Hubbard 1978; King 1986; Hendricks 1987a; Morton 2002; this study). The only exception is the White-throated Sparrow. Males of the "white-striped" morph feed nestlings less than females, but "tan-striped" males feed nestlings at about the same rate as do females (Kopachena and Falls 1993). Thus, the general pattern in *Zonotrichia* differs from that of most socially monogamous passerines, in which males feed nestlings as often as, or more frequently than, females (Johnson and Best 1982; Grundel 1987; Hegner and Wingfield 1987; Hendricks 1987b; Buitron 1988; Haggerty 1992), and nestling age has little effect on male feeding rates (Biermann and Sealy 1982; Breitwisch et al. 1986; Leffelaar and Robertson 1986; Moreno 1987). In relatively few monogamous passerines do males increase feeding rate with nestling age (Westneat 1988; Carey 1990).

In this study, male parental care varied among nests, especially those with nestlings < 3d. This variation could be due to age-related effects, with younger males provisioning young less frequently than older birds, although this effect has not been found in Yellow Warblers (*Dendroica petechia*) or American Redstarts (*Setophaga ruticilla*) (Studd and Robertson 1989; Omland and Sherry 1994). Alternatively, differences in male provisioning could be due either to genetic effects (Freeman-Gallant 1999) or to environmental factors such as weather (Rosa and Murphy 1994).

Because I did not study load size, which may be greater in male passerines (Moreno 1987), and because feeding nestlings is only one aspect of male PI during the nestling period (Breitwisch 1989; Carey 1990), I cannot conclude that total PI by male *Zonotrichia*

TABLE 2. Mean parental feeding rates (number/h) for Harris's Sparrows and White-crowned Sparrows according to sex and nestling age. Means based on averages for each brood within 3-d stages of the nestling period. Levels of significance (between sexes): * = P < 0.05; ** = $P < 0.01$ (Wilcoxon signed-ranks test).

	Harris's Sparrow			White-crowned Sparrow[a]	
Stage	Male	Female	*P*	Male	Female
Early (0-2 d)	0.48	4.33	**	0.75	3.44
Middle (3-5 d)	3.12	4.67	*	3.62	5.22
Late (6-8 d)	4.84	5.77	NS	6.17	7.64

[a] Sample sizes (see Figure 1) were too small for Wilcoxon signed-ranks test.

TABLE 3. Number of feedings/h/nest ($\bar{x} \pm$ SD) for male and female Harris's Sparrows according to brood size (all nestling ages pooled). Sample sizes (number of pairs) given in parentheses[1].

	Brood size		
Sex	3 (3)	4 (4)	5 (2)
Male	1.9 ± 0.4	3.0 ± 0.3	3.4 ± 0.1
Female	4.0 ± 0.3	4.8 ± 0.8	6.0 ± 0.4

[1] Two-factor ANOVA: Brood size: $df = 2$, $F = 9.86$, $P = 0.003$; sex: $df = 1$, $F = 30.96$, $P = 0.000$; interaction between sex and brood size: $df = 2$, $F = 0.18$, $P = 0.838$.

during the nestling period is less than for females. However, it is likely that reduced male care occurs during the early part of the nestling period because males made fewer visits to the nest during the early part of the nestling period and did not brood nestlings. Males might benefit from such a strategy because they could allocate more time and energy to extra-pair copulations or territory defense (Westneat 1988). Male *Zonotrichia* in some populations may engage in extra-pair copulations at relatively high rates (Sherman and Morton 1988; Tuttle 1993). However, opportunity for extra-pair copulations may be reduced for *Zonotrichia* at WG because breeding is highly synchronized and few females lay eggs when other pairs are feeding nestlings (Norment 1992). Thus reasons for reduced male attention to *Zonotrichia* nestlings at WG remain unclear. Possibly this behavioral pattern may have adaptive significance in more temperate habitats, and has persisted in an arctic environment because it is a conserved trait within the genus. Alternatively, the pattern may not be maladaptive in the ecological context existing at WG, or if it is maladaptive, recent development of the forest-tundra transition in northern Canada (Nichols 1976) means the trait has not had sufficient time to allow for modification through habitat-mediated selection.

Acknowledgments

The Frank M. Chapman Fund of the American Museum of Natural History; Panorama Fund of the Museum of Natural History and the Department of Systematics and Ecology, University of Kansas; Inland Bird Banding Association; Bill and Marilyn James; Gwen Norment; and Willetta and John Lueschen provided financial support. Doug Heard, Kevin McCormick, Peter and Teri Arychuck, and Dave and Kristen Olesen provided logistical support. Permits were issued by the Land Use Office, Department of Indian and Northern Affairs; Department of Renewable Resources, Government of the Northwest Territories (NWT); Science Institute of the NWT; and the Canadian Wildlife Service (Banding permit number 10539). Thanks to Martin Fuller, Paul Hendricks, Kevin Kimber, and Ken Wicker for help with field work. Melissa Norment provided support and encouragement throughout the project. John Hunter provided statistical advice. Drafts of the manuscript were reviewed by Paul Hendricks, John Hunter, Scott Sommershoe, and A. J. Erskine.

Literature Cited

Biermann, D. W., and **S. G. Sealy**. 1982. Parental feeding of nestling Yellow Warblers in relation to brood size and prey availability. Auk 99: 332-341.

Breitwisch, R. 1989. Mortality patterns, sex ratios, and parental investment in monogamous birds. Current Ornithology 6: 1-50

Breitwisch, R., **P. G. Merritt**, and **G. H. Whitesides**. 1986. Parental investment by the Northern Mockingbird: Male and female roles in feeding nestlings. Auk 103: 152-159.

Buitron, D. 1988. Female and male specialization in parental care and its consequences in Black-billed Magpies. Condor 90: 29-39.

Carey, M. 1990. Effects of brood size and nestling age on parental care by male Field Sparrows (*Spizella pusilla*). Auk 107: 580-586.

Chilton, G., **M. C. Baker**, **C. D. Barrentine**, and **M. A. Cunningham**. 1995. White-crowned Sparrow (*Zonotrichia leucophrys*). *In* The Birds of North America (183). *Edited by* A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D. C.

Custer, T. W., **R. G. Osborn**, **F. A. Pitelka**, and **J. A. Gessaman**. 1986. Energy budget and prey requirements of breeding Lapland Longspurs near Barrow, Alaska, U.S.A. Arctic and Alpine Research 18: 415-427.

DeWolfe, B. B. 1968, Nuttall's White-crowned Sparrow. U.S. National Museum Bulletin 237: 1292-1324.

Emlen, S. T., and **L. W. Oring**. 1977. Ecology, sexual selection, and the evolution of avian mating systems. Science 197: 215-233.

Falls, J. B., and **J. G. Kopachena**. 1994. White-throated Sparrow (*Zonotrichia albicollis*). *In* The Birds of North America, (128). *Edited by* A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Freeman-Gallant, C. R. 1999. Apparent heritability of parental care in Savannah Sparrows. Auk 116: 1132-1136.

Gowaty, P. A. 1996a. Field studies of parental care in birds: New data focuses on variation among females. Advances in the Study of Behavior 25: 476-531.

Gowaty, P. A. 1996b. Battles of the sexes and origins of monogamy. Pages 21-52, in Partnerships in birds. *Edited by* J. Black. Oxford University Press, New York.

Grundel, R. 1987. Determinants of nestling feeding rates and parental investment in the Mountain Chickadee. Condor 89: 319-328.

Haggerty, T. M. 1992. Effects of nestling age and brood size on nestling care in the Bachman's Sparrow (*Aimophila aestivalis*). American Midland Naturalist 128: 115-125.

Hare, F. K., and **M. K. Thomas**. 1974. Climate Canada. Wiley Publishers of Canada. Toronto.

Hegner, R. E., and **J. C. Wingfield**. 1987. Effects of brood size manipulations on parental investment, breeding success, and reproductive endocrinology of House Sparrows. Auk 104: 470-480.

Hendricks, P. 1987a. Breeding biology and nestling development of Golden-crowned Sparrows in Alaska. Wilson Bulletin 99: 693-696.

Hendricks, P. 1987b. Foraging patterns of Water Pipits (*Anthus spinoletta*) with nestlings. Canadian Journal of Zoology 65: 1522-1529.

Hubbard, J. D. 1978. Breeding biology and reproductive energetics of the Mt. White-crowned Sparrow in Colorado. Ph.D. dissertation, University of Colorado, Boulder.

Johnson, E. J., and **L. B. Best**. 1982. Factors affecting feeding and brooding of Gray Catbird nestlings. Auk 99: 148-156.

King, J. R. 1986. The daily activity period of nesting White-crowned Sparrows in continuous daylight at 65°N compared with activity periods at lower latitudes. Condor 88: 382-384.

Knapton, R. W., and **J. B. Falls**. 1983. Differences in contribution among pair types in the polymorphic White-throated Sparrow. Canadian Journal of Zoology 61: 1288-1292.

Kopachena, J. G., and **J. B. Falls**. 1993. Re-evaluation of morph-specific variations in parental behavior of the White-throated Sparrow. Wilson Bulletin 105: 48-59.

Leffelaar, D., and **R. J. Robertson**. 1986. Equality of feeding roles and the maintenance of monogamy in Tree Swallows. Behavioral Ecology and Sociobiology 18: 199-206.

Miller, A. H., and **V. D. Miller**. 1968. The behavioral ecology and breeding biology of the Andean Sparrow, *Zonotrichia capensis*. Caldasia 10: 84-154.

Moreno, J. 1987. Parental care in the Wheatear *Oenanthe oenanthe*: effects of nestling age and brood size. Ornis Scandinavica 18: 291-301.

Morton, M. L. 2002. The Mountain White-crowned Sparrow: migration and reproduction at high altitude. Studies in Avian Biology 24: 1-236.

Nichols, H. 1976. Historical aspects of the northern Canadian treeline. Arctic 29: 38-47.

Norment, C. J. 1985. Observations on the chronology for birds in the Warden's Grove area, Thelon River, Northwest Territories, 1977-1978. Canadian Field-Naturalist 99: 471-483.

Norment, C. J. 1992. Comparative breeding biology of Harris' Sparrows (*Zonotrichia querula*) and Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) in the Northwest Territories, Canada. Condor 94: 955-975.

Norment, C. J., and **S. A. Shackelton**. 1993. Harris' Sparrow (*Zonotrichia querula*). *In* The Birds of North America, (64). *Edited by* A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Norment, C. J., **P. Hendricks**, and **R. Santonocito**. 1998. Golden-crowned Sparrow (*Zonotrichia atricapilla*). *In* The Birds of North America, (352). *Edited by* A. Poole and F. Gill. The Birds of North America, Inc., Philadelphia, Pennsylvania.

Omland, K. E., and **T. W. Sherry**. 1994. Parental care at nests of two age classes of male American Redstart: Implications for female choice. Condor 96: 606-613.

Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pages 152-192, *in* Avian energetics. *Edited by* R. A. Paynter, Jr. Publications of Nuttall Ornithological Club 15. Cambridge, Massachusetts.

Rosa, S. M., and **M. T. Murphy**. 1994. Trade-offs and constraints on Eastern Kingbird parental care. Wilson Bulletin 106: 668-678.

Sherman, P. W., and **M. L. Morton**. 1988. Extra-pair fertilizations in Mountain White-crowned Sparrows. Behavioral Ecology and Sociobiology 22: 413-420.

Sokal, R. R., and **F. J. Rohlf**. 1981. Biometry. 2nd edition. W. H. Freeman, San Francisco, California.

Studd, M. V., and **R. J. Robertson**. 1989. Influence of age and territory quality on the reproductive behaviour of male Yellow Warblers. Canadian Journal of Zoology 67: 268-273.

Tuttle, E. M. 1993. Mate choice and stable polymorphism in the White-throated Sparrow. Ph.D. dissertation, State University of New York, Albany.

Underwood, A. J. 1997. Experiments in ecology. Cambridge University Press, New York, New York.

Walsberg, G. 1983. Avian ecological energetics. Pages 161-220, *in* Avian Biology, Volume 7. *Edited by* D. S. Farner, J. R. King, and K. C. Parkes. Academic Press, New York.

Westneat, D. F. 1988. Male parental care and extrapair copulations in the Indigo Bunting. Auk 105: 149-160.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100: 687-690.

Yasukawa, K., **J. L. McClure**, **R. A. Boley**, and **J. Zanocco**. 1990. Provisioning of nestlings by male and female Red-winged Blackbirds, *Agelaius phoeniceus*. Animal Behaviour 40: 153-166.

Zar, J. H. 1999. Biostatistical Analysis. 4th edition. Prentice-Hall Publishers, Englewood Cliffs, New Jersey.

Received 7 March 2001
Accepted 5 November 2003

The Shoreline Fringe Forest and Adjacent Peatlands of the Southern Central British Columbia Coast

ERIC G. LAMB[1] AND WILLIAM MEGILL[2]

Coastal Ecosystems Research Foundation (CERF) Allison Harbour, P.O. Box 124, Port Hardy, British Columbia V0N 2P0 Canada

[1]Current address: Department of Biology, University of Alberta, Edmonton, Alberta, T6G 2E9 Canada; e-mail: elamb@ ualberta.ca

[2]Current address: Centre for Biomimetic and Natural Technologies, Department of Mechanical Engineering, University of Bath, BA2 7AY, United Kingdom; e-mail: w.m.megill@bath.ac.uk

Lamb, Eric G., and William Megill. 2003. The shoreline fringe forest and adjacent peatlands of the southern central British Columbia coast. Canadian Field-Naturalist 117(2): 209-217.

Four distinct vegetation types are found in close proximity along an exposed section of the southern central coast of British Columbia. A coastal fringe of coniferous forest a few hundred metres wide is separated by a steep ecotone from an inland peatland-forest complex. The objectives of this study were (1) to describe the plant communities along the transition from forest to peatland, and (2) to identify some of the major environmental factors associated with those communities using indicator plant analysis. The coastal forest is dominated by *Thuja plicata*, *Tsuga heterophylla*, *Picea sitchensis,* and *Chamaecyparis nootkatensis*. Characteristic understory species include *Gaultheria shallon* and *Blechnum spicant*. Inland from the coastal forest are transitional forest stands with a species-rich understory including *Cornus canadensis, Hylocomium splendens,* and *Vaccinium parvifolium*. The peatlands are poor fens characterized by thickets of *Pinus contorta* and *Chamaecyparis nootkatensis* among open areas dominated by species such as *Sphagnum sp.*, *Empetrum nigrum*, *Juniperus communis*, and bogs characterized by *Myrica gale, Eriophorum angustifolium,* and *Sanguisorba officinalis*. Indicator plant analysis identified differences in the ground surface materials, soil moisture and nutrient regime between the vegetation types. The general trend is for an increase in soil moisture from the forest vegetation to the peatlands and a concurrent change from the Mor humus forms that dominate the coastal forest floor to the surface groundwater table of the peatlands. These environmental differences between forest and peatland are likely related to the steeper slopes typically found in the fringe forest vegetation.

Key Words: British Columbia central coast, ecotone, peatland, Indicator Species Analysis, Indicator Plant Analysis, Non-Metric Multidimensional Scaling, species distribution.

The Hecate Lowlands of the southern central British Columbia coast are dominated by a complex of dense coniferous forest and open peatlands. Along the outer coast, the peatlands are typically separated from the ocean by a narrow strip of dense coniferous forest. This coastal fringe forest is frequently less than 200 meters wide, terminating in a scrub forest ecotone separating it from the inland peatlands. The fringe forests of the British Columbia coast have rarely been discussed; most research on this vegetation type has been concentrated in southern Alaska (Zach 1950; Neiland 1971). The dominant peatland communities of the outer British Columbia coast have traditionally been classified as slope bogs (Banner et al. 1988), though more recent research indicates that in many cases they should be considered poor fens (Vitt et al. 1990). The successional relationships between forest and peatland in the region have been extensively studied (e.g., Zach 1950; Lawrence 1958; Ugolini and Mann 1979; Banner et al. 1983; Klinger et al. 1990), but only Neiland (1971) has carefully examined the ecotone between the forests and peatlands. The studies of the peatland-forest complex that have been done have rarely included sites directly exposed to the open ocean, leaving a major element of the coastal landscape very poorly understood. The fringe forests along exposed coastlines are also of interest because at many sites they have been subject to very little human disturbance, thus natural processes have not been influenced by human management practices.

This paper is an investigation into the vegetation patterns in the coastal fringe forests, adjacent peatlands, and the peatland-forest ecotone of a section of the southern Central Coast of British Columbia. The exposed coastlines of the region have been very poorly explored botanically, so the objectives of this study were (1) to identify the major plant communities along the transition from forest to peatland, and (2) to identify major environmental factors associated with those communities.

Study Area

The study area is a 30-km stretch of the southern central coast of British Columbia between Seymour Inlet and Smith Sound (51°02'N 127°31'W to 51°13'N 127°55'W). The region is provincially classified as the Coastal Western Hemlock biogeoclimatic zone (Pojar et al. 1991), and nationally as the Coastal Gap ecoregion of the Pacific Maritime ecozone (Marshall and Schut 1999*). The peatlands have traditionally been described as slope bog communities in the Pacific Oceanic Wetland Subregion (Banner et al. 1988),

though more recent work indicates that many sites receive nutrients from groundwater sources and therefore should be considered poor fens (Vitt et al. 1990).

The coastline is rugged, with a mixture of rocky cliffs, boulder beaches, and occasional sand beaches facing Queen Charlotte Strait. The land typically rises from the shore with moderate to steep slopes, but quickly flattens into rolling uplands dotted with bedrock outcrops. Substrates are typically intrusive igneous rock (Ryder 1978), and the soils moist to wet Ferro-Humic Podzols that rarely freeze in winter (Jungen and Lewis 1978). The climate is cool, wet, and windy. At the Egg Island light station (51°15'N 127°50'W) mean annual temperature is 8.2°C and mean annual precipitation is 2484 mm (Atmospheric Environment Service 1982*). Mean monthly temperature is lowest in January (3.4°C) and highest in August (13.4°C). Mean monthly precipitation ranges from 82 mm in July to 366 mm in December. Even in January only 10% of the precipitation falls as snow.

Methods

Field

Vegetation sampling for this study was carried out in the summer of 1999 along transects extending inland from 19 shoreline sites selected to represent a range of coastal features and wave exposure levels for an intertidal biodiversity study (Lamb et al. 2000*). All sites selected for this study are highly exposed and have low to moderate relief inland. At each study site a 300 m transect was laid out along a compass bearing approximately perpendicular to the shoreline. The shoreward end of the transect was located at the first vascular vegetation above the high tide line. Sampling was carried out at distances of 20 m, 50 m, 100 m, 200 m, and 300 m along the transect. The sampling intensity was greater in the first 100 m to capture the perceived rapid change in forest composition very near the shore. Intervals were increased between quadrats toward the inland end of the transects, where the change in composition was slower, to ensure that the full range of vegetation, from coastal forest to inland peatland, could be sampled in one day. At each location pairs of 2 m by 2 m quadrats were placed 10 m to either side of the transect, for a total of 190 quadrats. Each quadrat was surveyed for bryophytes, herbaceous plants, and shrubs. Vascular plants were identified to species with the exception of some difficult genera such as *Carex* and *Listera*; bryophytes were identified to genus with the exception of *Hylocomium splendens*. Percent cover was estimated using the Braun-Blanquet six-point cover scale (Kent and Coker 1992). Nomenclature follows Douglas et al. (1998; 1999; 2000; 2001; 2002) for vascular plants and Schofield (1992) for the bryophytes. Shrubs and small trees included any woody plant less than 5 cm DBH (diameter at breast height). Four trees greater than 5 cm DBH surrounding each plot were sampled using the point-quarter method (Krebs 1989).

Data Analysis

The overall trends in these data were examined using a Non-Metric Multidimensional Scaling (NMS) ordination. NMS is a non-parametric ordination method well suited to community data because it avoids many of the assumptions about the underlying structure of the data made by traditional ordination methods (Kenkel and Orlóci 1986; McCune and Grace 2002). The autopilot program in the PC-Ord program (McCune and Mefford 1999), with the slow and thorough analysis option, Sorenson distance, and the default settings selected, was used for the analysis. Rare species (observed in fewer than five quadrats) were eliminated prior to analysis.

Since four broad vegetation types were subjectively observed during fieldwork, quadrats were classified into four groups using a hierarchical cluster analysis (Ward's Method using Euclidean distance). Ward's method is recommended as an effective classification tool for community data (McCune and Grace 2002). Species that were significantly more frequent and abundant in each of the four groups of quadrats were identified using Indicator Species Analysis (Dufrêne and Legendre 1997). Indicator values are calculated by multiplying the relative abundance of each species in a particular group by the relative frequency of the species' occurrence in that group. The significance of the observed indicator values are evaluated using a Monte Carlo simulation of 1000 runs where samples are randomly reassigned to groups and indicator values recalculated. PC-Ord (McCune and Mefford 1999) was used for these analyses.

Tree stem density, mean basal area per stem, and species importance values were calculated for each vegetation type. Tree density and 95% confidence limits were calculated from the Point-Quarter data following Krebs (1989). The Importance Values for each tree species in each vegetation type were calculated following Kent and Coker (1992). Importance values are the sum of the relative density (number of individuals of a species/total number of individuals)$\times$100, the relative dominance (mean basal area per tree of a species$\times$number of trees of that species)/(mean basal area per tree of all species/total number of trees)$\times$100, and the relative frequency (proportion of plots containing a species)$\times$100. Ln-transformed mean basal area per stem (of the four stems measured at each plot) was compared between the four vegetation types using an ANOVA followed by a post-Tukey test. Only basal area was compared using ANOVA since the measures of density and Importance Values are aggregate values calculated from all of the plots in a vegetation type, and hence cannot be compared using statistical tests such as ANOVA.

The environmental conditions of the four vegetation types were explored using the spectral method of Indicator Plant Analysis (Klinka et al. 1989). Indicator plant analysis is based on the observation that many species require very specific environmental conditions

and that the presence of a group of species with similar tolerances in high abundance at a site is a strong indication that those conditions prevail at that site. Indicator plant analysis was used as an alternative to costly and labor-intensive soil sample collection and analysis. Indicator species analysis can be used to estimate the soil moisture regime (MOIST), soil nutrient regime (NITR), and the type of ground surface materials present (GSM). Each environmental factor is divided into several categories, or "Indicator Plant Groups"; species with a relatively narrow range of tolerance for that environmental factor are assigned to the appropriate Indicator Plant Group. Species with wide tolerances for a particular factor are generally not used as indicators. Klinka et al. (1989) provide extensive lists of species from coastal British Columbia that fall into the Indicator Plant Groups for each environmental factor.

There are four steps to an indicator plant analysis. First, the mean abundance for each species across all of the quadrats in each vegetation type is calculated. Second, the species are divided into their respective indicator plant groups, and the abundances of all species belonging to each group are summed. Third, the proportion of the total species abundance in each vegetation type that each indicator plant group makes up is calculated. Finally, these proportions are used to estimate the actual range of values that an environmental factor takes in a vegetation type by following the tables and keys provided in Klinka et al. (1989). A reliability ratio, or the proportion of species in a vegetation type, that are useful as indicators for a particular environmental variable is calculated. A low reliability ratio indicates that many of the species in a community either are generalists or have not been screened for their potential as indicators.

Slope was compared between the coastal forest and the transition and peatland vegetation types. Direct measurements of slope were not taken in the field, so estimates from large-scale topographic maps were used instead. The average percent slope was estimated along each transect from the distance between 20 m contour intervals on 1:20 000 Terrain Resource Inventory Maps (TRIM). Each quadrat was assigned the slope estimated for that segment of the transect. Quadrats that fell on a contour line were assigned the average of the slopes of the segments above and below them. Mean slopes were compared between the four vegetation types using a one-way ANOVA followed by a post-hoc Dunnet's T3 test. Variances were unequal and could not be improved by transformation, so the post-hoc T3 test, which does not assume equal variances, was used instead of a Tukey test (Day and Quinn 1989).

Results and Discussion

Nineteen sites and 190 quadrats were sampled in the field. The NMS produced a 2-dimensional solution with a final stress of 19.655 (Figure 1). The first ordination axis accounts for 46.7% of the variation in the species data and the second 35.8% for a cumulative r^2 of 0.825. Species with a substantial amount of variation (r^2>0.100) explained by at least one of the two axes are listed in Table 1. The first axis separates quadrats with a high abundance of *Gaultheria shallon* and *Rhytidiadelphus* sp. from quadrats with a high abundance of *Eriophorum angustifolium, Juniperus communis, Myrica gale, Sphagnum* sp., and *Trichophorum caespitosum.* The second axis separates quadrats with a high abundance of *Blechnum spicant, Gaultheria shallon, Kindbergia* sp., and *Plagiothecium* sp. from quadrats with a high abundance of *Empetrum nigrum, Eriophorum angustifolium, Juniperus communis, Kalmia microphylla, Ledum groenlandicum, Myrica gale, Pinus contorta, Sphagnum* sp., and *Trichophorum caespitosum.* Together these two axes delineate a clear gradient from forest vegetation to open peatland. Since the two axes explain a large proportion of the variation in the species data (r^2=0.825), this ecotone is the major feature of this community.

The cluster analysis divided the quadrats into four groups corresponding to the four vegetation zones subjectively observed in the field (Figure 1). With few exceptions, the quadrats classified into each vegetation type are closely grouped together in the ordination diagram. The Coastal Fringe Forest type has a closed canopy of large trees with a dense to open shrub and bryophyte dominated understory. The Transitional Forest type has an open canopy with a very extensive shrub understory. The Dry Peatland type supports small thickets of trees among open ericaceous heaths, while the Wet Peatland type is dominated by *Myrica gale.* The majority (87%) of the quadrats surveyed 20 m and 50 m from the shore were classified as Fringe Forest. The transition between forest and peatland generally fell between 100 m and 300 m from the shore, while at eleven sites Fringe Forest vegetation was present at the inland end of the transect.

Species that are significantly more frequent and abundant in the understory plant community of one of the four vegetation types are summarized in Table 2. The Coastal Fringe Forest understory is dominated by a mixture of ericaceous shrubs, ferns, and bryophytes. Common species include *Blechnum spicant, Gaultheria shallon, Rubus pedatus,* and several bryophytes including *Kindbergia* sp., *Hookeria* sp., and *Plagiothecium* sp. In contrast, species such as *Ledum groenlandicum, Fauria crista-galli, Kalmia microphylla, Trichophorum caespitosum, Myrica gale, Juniperus communis, Eriophorum angustifolium* and *Sphagnum* sp. dominate the peatlands. The majority of the species characteristic of the Fringe Forest and the peatlands co-occur in the Transitional Forest, and several common species, including *Cornus canadensis, Hylocomium splendens, Linnaea borealis,* and *Maianthemum dilatatum,* are significantly more frequent and abundant there.

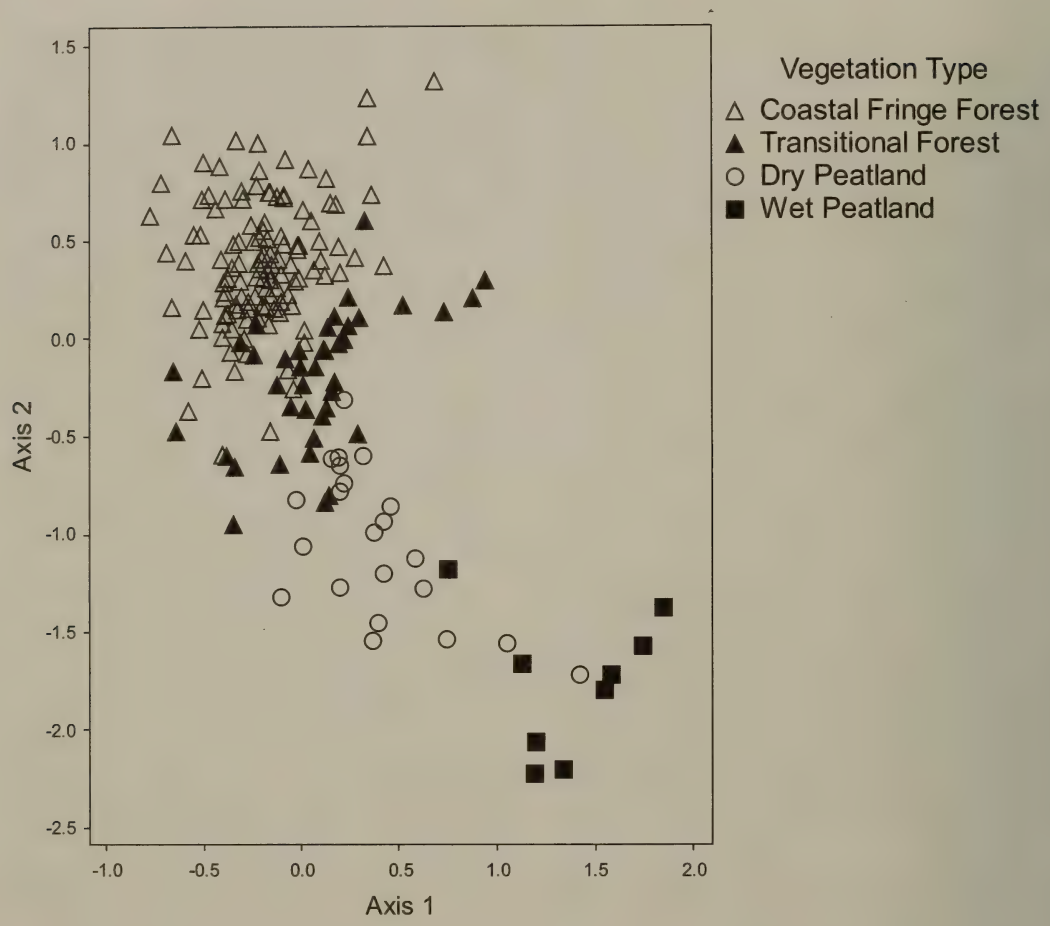


FIGURE 1. NMS ordination of the plant cover data with the four vegetation types from the cluster analysis overlain.

The plant communities identified in the classification are similar to the south-east Alaska plant communities described by Neiland (1971). For example, she described a forest community found on steeper slopes fronting the ocean that had many understory species, including *Rhytidiadelphus* sp. and *Vaccinium parvifolium*, in common with the Coastal Fringe and Transitional forest types. The Transitional Forest and the Dry Peatland types observed in this study should be classified as types of slope bog (Banner et al. 1988), but the frequency of *Chamaecyparis nootkatensis* in those vegetation types (Table 2; 3) indicates that this classification may be incorrect. *C. nootkatensis* is an indicator of soligenous fens that receive mineral nutrients from groundwater sources in addition to rain deposition (Vitt et al. 1990), suggesting that many of the peatlands on the central coast may be poor fens. The species composition of the Wet Peatland community is consistent with the slope bog descriptions in Banner et al. (1988), and the absence of *C. nootkatensis* from this vegetation type indicates that this vegetation type should be considered a true bog.

There is a significant decline in mean basal area per stem ($F=16.812$; $P<0.001$) from the Coastal Fringe Forest to the peatlands (Figure 2). Stem densities, however, are very similar between the Fringe Forest, Transitional Forest, and Dry Peatland vegetation types (Figure 2). The large confidence intervals around mean basal area in the Transitional Forest, and especially in the Coastal Fringe Forest, reflect the great variation in tree sizes found there. For example, the diameters of the largest individuals of the four major tree species observed were *Chamaecyparis nootkatensis* (0.65 m), *Picea sitchensis* (1.67 m), *Thuja plicata* (1.49 m), and *Tsuga heterophylla* (1.03 m). Small, suppressed individuals were common in the understory and vigorous saplings were common in canopy gaps. The Dry Peatland supports many of the same tree species as the Transitional forest, but *Pinus contorta* is much more important. The Wet Peatland vegetation is characterized

TABLE 1. Species axis scores and Pearson correlations between species abundance and axis scores from the NMS ordination. Only species with an $r^2>0.100$ on at least one axis are listed.

Species	Common Name	Axis 1			Axis 2		
		Score	r	r^2	Score	r	r^2
Blechnum spicant	Deer Fern	-0.116	-0.253	0.064	0.300	0.427	0.182
Chamaecyparis nootkatensis	Yellow Cedar	0.170	0.128	0.016	-0.791	-0.389	0.152
Drosera rotundifolia	Round -Leafed Sundew	0.383	0.173	0.03	-1.138	-0.335	0.113
Empetrum nigrum	Crowberry	0.329	0.308	0.095	-1.047	-0.64	0.409
Eriophorum angustifolium	Narrow-Leafed Cotton Grass	1.364	0.611	0.373	-1.722	-0.504	0.254
Fauria crista-galli	Deer Cabbage	0.397	0.253	0.064	-1.024	-0.427	0.182
Gaultheria shallon	Salal	-0.137	-0.58	0.336	0.255	0.702	0.493
Grass		0.146	0.149	0.022	-0.486	-0.324	0.105
Juniperus communis	Common Juniper	0.988	0.642	0.412	-1.608	-0.683	0.467
Kalmia microphylla	Bog Laurel	0.582	0.473	0.223	-1.219	-0.647	0.418
Kindbergia sp.		-0.010	-0.278	0.077	0.291	0.528	0.279
Ledum groenlandicum	Labrador Tea	0.124	0.162	0.026	-0.710	-0.606	0.367
Myrica gale	Sweet Gale	1.113	0.679	0.461	-1.498	-0.597	0.356
Oxycoccus oxycoccos	Bog Cranberry	0.878	0.327	0.107	-1.341	-0.327	0.107
Pinus contorta	Shore Pine	0.526	0.347	0.12	-1.262	-0.543	0.295
Plagiothecium sp.		-0.115	-0.242	0.059	0.303	0.417	0.174
Racomitrium sp.		0.668	0.364	0.133	-1.565	-0.558	0.311
Rhytidiadelphus sp.		-0.126	-0.434	0.189	0.147	0.331	0.109
Sanguisorba officianalis	Great Burnet	1.424	0.68	0.462	-1.699	-0.53	0.281
Sphagnum sp.		0.432	0.66	0.436	-0.644	-0.643	0.413
Tofieldia glutinosa	Sticky False Asphodel	0.836	0.358	0.128	-1.626	-0.455	0.207
Trichophorum caespitosum	Tufted Clubrush	0.958	0.606	0.367	-1.546	-0.638	0.408
Trientalis arctica	Northern Starflower	0.707	0.288	0.083	-1.490	-0.396	0.157
Vaccinium sp.		0.437	0.191	0.037	-1.330	-0.38	0.145
Vaccinium uliginosum	Bog Blueberry	0.893	0.338	0.114	-1.644	-0.406	0.165
Vaccinium vitis-idaea	Lingonberry	-0.001	-0.001	0	-0.502	-0.394	0.155

by scattered "bonsai" *Pinus contorta*. The Coastal Fringe Forest tree community is more species rich than the other vegetation types, as small numbers of *Taxus brevifolia* and *Malus fusca* were sampled there and individuals of two much rarer species, *Abies amabilis* and *Alnus rubra,* were encountered.

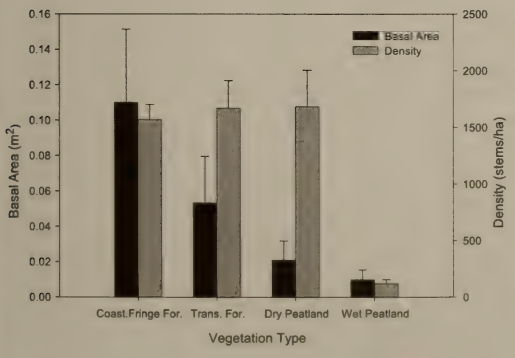


FIGURE 2. Stem density/ha and basal area/stem in each vegetation type. Basal areas were significantly larger ($p < 0.05$) in the Coastal and Transitional forests than in the Peatland types. Error bars are 95% confidence intervals.

Indicator plant analysis was performed to estimate the soil moisture regime, soil nutrient regime, and ground surface materials found in the four vegetation types (Table 3). The MOIST6 soil indicator group is dominant in all but the Coastal Fringe Forest, indicating an overall wet moisture regime. In the Fringe Forest the MOIST4 group is dominant and the MOIST5 group well represented, indicating a moist soil moisture regime. A moist regime is found on sites where water deficits do not normally occur and the groundwater table is normally between 30 and 60 cm deep or deeper (Klinka et al. 1989). Species from other indicator plant groups are also found, such as the MOIST2 group solely represented in the Wet and Dry Peatlands by *Juniperus communis*. Species from the GSM1 group, indicating Mor humus forms, or a layer of compacted organic material greater than 5 cm thick overlying the mineral soil, were present in all four vegetation types. These species were dominant in all but the Wet Peatland type. Species from the GSM5 group, indicating a surface groundwater table, were dominant in the Wet Peatland and well represented in the Dry Peatland. The NITR1 group (indicating poor to very poor soils) is dominant in the Fringe Forest, Transitional Forest, and Dry Peatland vegetation types, and well represented in the Wet Peatland. The NITR2 group (indicating medium soils) is dominant in the

TABLE 2. Indicator Values (IV) of common understory species significantly more frequent and abundant ($P < 0.100$) in one of the four vegetation types. Species are grouped by the vegetation types in which they have the highest indicator values. The maximum possible observed indicator value is 100. The mean randomized indicator values are calculated for the group with the highest observed indicator value from a Monte-Carlo simulation of 1000 runs. The P-value is the proportion of the randomized runs that produced an indicator value higher than the observed indicator value.

		Observed Indicator Values						
Species	Common Name	Fringe Forest	Trans. Forest	Dry Peatland	Wet Peatland	Rand IV	SD Rand IV	P
Coastal Fringe Forest								
Blechnum spicant	Deer Fern	37	18	4	0	20.7	4.24	0.008
Gaultheria shallon	Salal	47	35	13	0	26.8	2.03	<0.001
Hookeria sp.		18	3	0	0	10.2	4.47	0.057
Kindbergia sp.		47	28	7	0	25.4	3.28	<0.001
Leafy Liverwort		32	14	1	1	19.7	4.29	0.018
Plagiothecium sp.		40	31	1	0	23.3	4.26	0.006
Rhizomnium sp.		22	18	0	0	15.6	4.63	0.084
Rubus pedatus	Five-leafed Bramble	17	2	0	0	9.7	4.51	0.069
Transitional Forest								
Cornus canadensis	Bunchberry	16	38	27	3	24.5	3.53	0.002
Dicranum sp.		19	27	19	0	21.8	3.96	0.091
Hylocomium splendens		25	42	11	0	23.8	3.94	0.002
Linnaea borealis	Twinflower	6	29	26	0	16.9	4.44	0.019
Maianthemum dilatatum	False Lily-of-the-Valley	13	31	7	0	17.6	4.42	0.017
Menziesia ferruginea	False Azalea	28	32	0	0	19.3	4.66	0.029
Rhytidiadelphus sp.		38	39	15	0	26.3	2.59	<0.001
*Thuja plicata**	Western Red Cedar	6	24	16	0	14.7	4.59	0.049
Vaccinium parvifolium	Red Huckleberry	28	36	3	0	22.1	4.23	0.007
Herbertus sp.		0	15	3	0	7.2	3.97	0.046
Thallose Liverworts		0	11	0	0	5.5	3.19	0.051
Dry Peatland								
Carex pauciflora	Few-Flowered Sedge	0	1	15	2	5.1	3.09	0.018
*Chamaecyparis nootkatensis**	Yellow Cedar	0	10	29	0	8.8	4.28	0.005
Drosera rotundifolia	Round-Leafed Sundew	0	2	15	9	6.3	3.72	0.042
Empetrum nigrum	Crowberry	0	3	57	17	11	4.52	<0.001
Fauria crista-galli	Deer Cabbage	0	1	19	14	7.5	3.98	0.028
Kalmia microphylla	Western Bog Laurel	0	0	48	30	9.2	4.25	<0.001
Ledum groenlandicum	Labrador Tea	0	16	47	9	14	4.47	<0.001
Microseris borealis	Apargidium	0	0	27	0	4.7	3.22	0.002
Oxycoccus oxycoccos	Bog Cranberry	0	0	17	3	4.7	3.07	0.015
Pteridium aquilinum	Bracken Fern	3	11	22	0	12.1	4.64	0.050
Trientalis arctica	Northern Starflower	0	0	13	10	4.9	3.02	0.035
Vaccinium sp.		0	0	36	0	5.2	3.32	<0.001
Vaccinium vitis-idaea	Lingonberry	0	33	44	0	13.8	4.36	0.002
Lycopodium clavatum	Running Clubmoss	0	0	14	0	3.5	2.41	0.004
Wet Peatland								
Carex sp.		4	7	13	26	14.6	4.45	0.032
Eriophorum angustifolium	Narrow-Leafed Cotton Grass	0	0	1	71	5.8	3.58	<0.001
Juniperus communis	Common Juniper	0	0	9	70	7.5	4.1	<0.001
Myrica gale	Sweet Gale	0	0	4	84	7.1	4.17	<0.001
Pinus contorta	Shore Pine	0	0	26	26	7.7	4.24	0.005
Racomitrium sp.		0	0	12	37	6.8	4.26	0.002
Sanguisorba officinalis	Great Burnet	0	0	0	96	6.1	3.73	<0.001
Sphagnum sp.		0	22	34	37	16.4	4.3	0.003
Tofieldia glutinosa	Sticky False Asphodel	0	0	3	35	5.2	3.17	<0.001
Trichophorum caespitosum	Tufted Clubrush	0	0	10	58	7.2	3.99	<0.001
Vaccinium uliginosum	Bog Blueberry	0	0	8	32	5.5	3.34	<0.001

Wet Peatland. These values indicate a poor nutrient regime in the Fringe Forest and Dry Peatland, poor to very poor in the Transitional Forest, and very poor in the Wet Peatland (Klinka et al. 1989).

The indicator plant analysis provides a general outline of the environmental conditions in each of the four vegetation types, but due to the low reliability ratios the results should be considered very preliminary. The

TABLE 3. Relative importance values (relative density + relative dominance + relative frequency) for each of the tree species found in each of the four vegetation types. These values reflect the prominence of a particular species in a vegetation type relative to the other species; large values do not necessarily indicate high overall stem density or basal area per stem.

Species	Coastal Forest	Transitional Forest	Dry Peatland	Wet Peatland
Alnus crispa (Sitka Alder)	4.23	0	0	0
Chamaecyparis nootkatensis (Yellow Cedar)	35.65	75.73	87.31	0
Malus fusca (Pacific Crab-Apple	2.81	0	0	0
Picea sitchensis (Sitka Spruce)	53.23	22.71	0	0
Pinus contorta (Shore Pine)	16.78	18.20	125.23	233.39
Snag	99.49	97.38	132.42	110.46
Taxus brevifolia (Pacific Yew)	2.19	0	0	0
Thuja plicata (Western Red Cedar)	116.89	133.55	78.84	33.93
Tsuga heterophylla (Western Hemlock)	128.73	126.78	48.91	0

reliability ratios are low due to the sampling procedure, as many of the species only identified to genus could not be used as indicators. Two genera that were not identified to species, *Carex* and *Sphagnum*, are often good indicators of environmental conditions in peatlands (Klinka et al. 1989). These species made up a substantial proportion of the cover in this study, and their inclusion in the indicator plant analysis would substantially increase the reliability ratios. It is unlikely, however, that the trends in environmental conditions identified in the indicator species analysis would be altered if more species were included. The species of *Carex* and *Sphagnum* that we most likely encountered in the peatlands are indicators of conditions similar to those suggested by the forb and shrub species.

The most general environmental trend over the forest – peatland transition is an increase in soil moisture levels. This increase correlates with the indications for ground surface materials. Those show a distinct change from the Mor humus forms that dominate the Fringe Forest floor to the surface groundwater table of the Wet Peatland. The only anomaly in the moisture trend is the occurrence of the MOIST2 indicator plant group (moderately to very dry) in the Wet and Dry Peatlands. This group is represented solely by *Juniperus communis,* and illustrates the environmental heterogeneity found at small scales in these habitats. The lowest areas of the Wet Peatland frequently develop standing pools of water during rainy weather, but among the pools are hummocks and small hillslopes that support *Juniperus communis* in the otherwise wet habitat. Vitt et al. (1990) found *Juniperus* in similar raised habitats on the northern British Columbia coast. In contrast to the other environmental factors, there are no clear trends in the soil nutrient regime between the four vegetation types. It is clear that the overall soil nutrient regime in the study area is poor to very poor, but finer differences between the vegetation types cannot be clearly distinguished. The source of water at any particular site in the peatlands (groundwater vs. rainwater) is important (Vitt et al. 1990), and it is likely that a great deal of small-scale variation within each vegetation type is due to small differences in drainage.

Mean estimated slopes were significantly higher in the Fringe and Transitional forests than in the peatlands ($F=3.179$; $P=0.012$) (Figure 3). These steeper slopes in the forested vegetation types are in accord with the observations of Zach (1950) and Neiland (1971). For example, Neiland (1971) found that the mean slope of sites in the coastal forest was approximately 30% with some sites occurring on slopes of up to 60%. In contrast, she found ecotonal bog-forests generally to be on slopes between 15% and 20% to a maximum of 40%, and bogs generally on slopes of less than 10%. Those authors considered increased drainage on the steeper slopes to be the major environmental factor distinguishing forest from peatland vegetation, a conclusion supported by the drier Fringe Forest soils (Table 3). Better drainage on steeper slopes is clearly not a complete answer, as Banner et al. (1988) report that treed slope bogs can be found on slopes of up to 70%. Soil saturation resulting from *Sphagnum* development (Lawrence 1958) and the development of soil layers that limit drainage (Ugolini and Mann 1979) have been proposed as mechanisms for the conversion of forest to bog along the Pacific Coast. It is likely that long-term

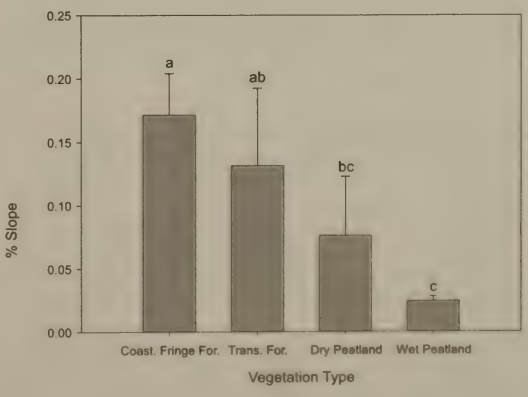


FIGURE 3. Mean slope in each of the four vegetation types. Error bars are 95% confidence intervals, and letters indicate significant differences ($P < 0.05$).

TABLE 4. Percentage of the total species abundance in each vegetation type comprised of species that fall into separate Indicator Plant Groups for three main environmental factors: soil moisture (MOIST), soil nutrients (NITR), and ground surface materials (GSM). The explanation of each indicator plant group describes the range of environmental conditions to which species belonging to that group are typically associated. The reliability ratio (Rel Ratio) is the proportion of the total species abundance in a particular vegetation type that is made up by species that are useful as indicators for that environmental factor (Klinka et al. 1989).

Indicator Group	Coastal Forest	Transitional Forest	Dry Peatland	Wet Peatland	Explanation
MOIST 1	0	0	0	0	very to excessively dry
MOIST 2	0	0.05	8.70	23.58	moderately to very dry
MOIST 3	3.79	12.14	5.52	0	fresh to moderately dry
MOIST 4	69.53	36.03	3.73	0.25	very moist to fresh
MOIST 5	16.53	10.31	28.34	19.62	wet to very moist
MOIST 6	10.15	41.47	53.71	56.54	very wet to wet
Rel Ratio	0.19	0.14	0.26	0.57	
NITR 1	90.13	92.91	80.58	37.15	very poor to poor
NITR 2	0.05	0.59	10.35	62.80	medium
NITR 3	9.82	6.51	9.07	0.05	rich to very rich
Rel Ratio	0.57	0.42	0.43	0.60	
GSM 1	89.8	81.94	57.97	11.70	Mor humus forms
GSM 2	6.77	3.59	8.95	0.06	Moder and Mull humus forms
GSM 3	0	0	0	0	exposed mineral soils
GSM 4	0.03	0	0	0	shallow soil over bedrock fragments
GSM 5	3.41	14.46	33.08	88.25	surface groundwater table
Rel Ratio	0.56	0.40	0.43	0.45	

successional processes associated with climactic variations and soil changes have a strong influence on the local disposition of forest and peatland vegetation at any particular site.

Acknowledgments

This work was funded by research grants from the Department of Fisheries and Oceans and the Coastal Ecosystems Research Foundation, and an employment grant from the British Columbia Ministry of Environment, Lands, and Parks (E-Team). A. Walkus Jr., B. Kaytor, and A. Hanuse assisted with data collection. Y. Dolmat, C. Metti, N. Witherly, and B. Woodward provided logistical support. G. Bradfield and two anonymous reviewers provided many helpful comments on earlier versions of this paper.

Documents Cited (marked * in text citations)

Atmospheric Environment Service. 1982. Canadian Climate Normals 1951-1980 Temperature and Precipitation: British Columbia.

Lamb, E. G., Y. Dolmat, J. Holloway, K. Shankel, and **W. Megill.** 2000. Findings of the 1999 CERF Survey of Coastal Biodiversity on the Central Coast of British Columbia. Unpublished Report to DFO [Department of Fisheries and Oceans]. 114 pages.

Marshall, I. B., and **P. H. Schut**. 1999. A national ecological framework for Canada. Ecosystems Science Directorate, Environment Canada, and Research Branch, Agriculture and Agri-Food Canada.

Literature Cited

Banner, A., R. J. Hebda, E. T. Oswald, J. Pojar, and **R. Trowbridge.** 1988. Wetlands of Pacific Canada. Pages 304-346 *in* Wetlands of Canada. *Edited by* National Wetlands Working Group, Polyscience, Ottawa. 452 pages.

Banner, A., J. Pojar, and **G. E. Rouse.** 1983. Postglacial paleoecology and successional relationships of a bog woodland near Prince Rupert, British Columbia. Canadian Journal of Forest Research 13: 938-947.

Day, R. W., and **G. P. Quinn**. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59: 433-463.

Douglas, G. W., D. Meidinger, and **J. Pojar**. *Editors*. 1998, 1999, 2000, 2001, 2002. The Illustrated Vascular Plants of British Columbia. (8 Volumes). Province of British Columbia, Victoria.

Dufrêne, M., and **P. Legendre.** 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345-366.

Jungen, J. R., and **T. Lewis.** 1978. The Coast Mountains and islands. Pages 102-120 *in* The soil landscapes of British Columbia. *Edited by* K. W. G. Valentine, P. N. Sprout, T. E. Baker, and L. M. Lavkulich. Resource Analysis Branch, Ministry of the Environment, Victoria, British Columbia. 197 pages.

Kenkel, N. C., and **L. Orlóci**. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. Ecology 67: 919-928

Kent, M., and **P. Coker.** 1992. Vegetation description and analysis. John Wiley and Sons, West Sussex. 363 pages.

Klinger, L. F., S. A. Elias, V. M. Behan-Pelletier, and **N. E. Williams.** 1990. The bog climax hypothesis: fossil arthropod and stratigraphic evidence in peat sections from southeast Alaska, USA. Holarctic Ecology 13: 72-80.

Klinka, K., V. J. Krajina, A. Ceska, and **A. M. Scagel.** 1989. Indicator plants of coastal British Columbia. UBC Press, Vancouver, British Columbia. 288 pages.

Krebs, C. J. 1989. Ecological methodology. Harper Collins Publishers, New York. 654 pages.

Lawrence, D. B. 1958. Glaciers and vegetation in southeastern Alaska. American Scientist 46: 89-122.

McCune, B., and **J. B. Grace.** 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B., and **M. J. Mefford**. 1999. PC-ORD: Multivariate analysis of ecological data. MjM Software Design, Gleneden Beach, Oregon.

Neiland, B. J. 1971. The forest-bog complex of southeast Alaska. Vegetatio 22: 1-64.

Pojar, J., K. Klinka, and **D. A. Demarchi.** 1991. Coastal Western Hemlock Zone. Pages 95-111 *in* Ecosystems of British Columbia. *Edited by* D. Meidinger, and J. Pojar. BC Ministry of Forests, Research Branch, Victoria. 380 pages.

Ryder, J. M. 1978. Geology, landforms, and surficial materials. Pages 11-34 *in* The soil landscapes of British Columbia. *Edited by* K. W. G. Valentine, P. N. Sprout, T. E. Baker, and L. M. Lavkulich. Resource Analysis Branch, Ministry of the Environment, Victoria, British Columbia. 197 pages.

Schofield, W. B. 1992. Some Common Mosses of British Columbia. Royal British Columbia Museum, Victoria, British Columbia. 394 pages.

Ugolini, F. C., and **D. H. Mann.** 1979. Biopedological origin of peatlands in South East Alaska. Nature 281: 366-369.

Vitt, D. H., D. G. Horton, N. G. Slack, and **N. Malmer.** 1990. *Sphagnum* dominated peatlands of the hyperoceanic British Columbia Coast: patterns in surface water chemistry and vegetation. Canadian Journal of Forest Research 20: 696-711.

Zach, L. W. 1950. A northern climax, forest or muskeg? Ecology 31: 304-306.

Received 9 March 2001
Accepted 8 December 2003

Space and Habitat Use by Male and Female Raccoons, *Procyon lotor*, in Kansas

JAN F. KAMLER[1] AND PHILIP S. GIPSON

Kansas Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, 205 Leasure Hall, Division of Biology, Kansas State University, Manhattan, Kansas 66506 USA
[1]Present address: Polish Academy of Sciences, Mammal Research Institute, 17-230 Bialowieza, Poland

Kamler, Jan F., and Philip S. Gipson. 2003. Space and habitat use by male and female Raccoons, *Procyon lotor*, in Kansas. Canadian Field-Naturalist 117(2): 218-223.

We monitored 12 radio-tagged adult Raccoons (*Procyon lotor*) from an unexploited population in northeastern Kansas to determine intersexual differences in space and habitat use. Home ranges (mean ± SE) of males were relatively large (266 ± 14 ha) and mutually exclusive, whereas home ranges of females were relatively small (122 ± 52 ha) and overlapped extensively. Sizes of home ranges were smaller ($P < 0.05$) in winter than summer for both sexes, although females reduced their home ranges more than males. Females used more grassland habitats than males during summer ($P < 0.05$), whereas males used more grassland habitats than females during winter ($P < 0.05$). Seasonal differences in habitat selection was detected for females ($P < 0.05$), but not males. Intersexual differences in space and habitat use were likely related to different behavioral strategies employed by male and female Raccoons.

Key Words: *Procyon lotor*, Raccoon, habitat selection, home range, Kansas.

Raccoons (*Procyon lotor*), like most solitary carnivores, exhibit intersexual differences in home range sizes and spacing patterns (Kaufmann 1982; Sanderson 1987; Sandell 1989), with male home ranges larger than those of females (Fritzell 1978a; Sherfy and Chapman 1980; Lehman 1984; Seidensticker et al. 1988; Gehrt and Fritzell 1997). Although Raccoons exhibit sexual dimorphism, the large size of male home ranges cannot be explained by energetics alone (Gehrt and Fritzell 1997). Intersexual differences in home ranges and spacing patterns of Raccoons are likely related to different behavioral tactics employed by male and female Raccoons (Sandell 1989; Gehrt and Fritzell 1997, 1998). Little is known about intersexual differences in habitat use by Raccoons. Because different behavioral strategies employed by male and female Raccoons have been shown to affect home range sizes and spacing patterns, behavioral differences might also affect habitat use. Additionally, Raccoons are known to decrease activity during winter, especially in more northern latitudes, as ambient temperatures and food resources decrease (Schneider et al. 1971; Glueck et al. 1988). However, it is not known if male and female Raccoons respond differently to seasonal changes in temperature and food availability.

Although there have been numerous studies of Raccoons, few occurred in unexploited populations (Seidensticker et al. 1988; Gehrt and Fritzell 1997). To better understand evolutionary significant situations among carnivores, research is needed on unexploited populations in native habitats (Crabtree and Sheldon 1999). Finally, Raccoons are generally considered to be arboreal, yet little is known about Raccoon ecology within prairie-dominated ecosystems of the Great Plains.

The objectives of this study were to determine sexual and seasonal differences in home range sizes and habitat use of Raccoons from an unexploited population in a prairie-dominated ecosystem in northeastern Kansas. We tested the null hypotheses that (1) there were no seasonal differences in home range sizes between sexes, (2) there were no seasonal differences in home range sizes within sexes, (3) there were no seasonal differences in habitat use between sexes, and 4) there were no seasonal differences in habitat use within sexes.

Study Area

This study was conducted on Fort Riley Military Reservation (Fort Riley) in Geary, Riley and Clay counties, Kansas (39°11'N, 96°77'W). Fort Riley is a 40,273-ha permanent U.S. Army Forces Command installation located in the Flint Hills Region of northeastern Kansas. The vegetative community is dominated by tall and mixed-grass prairie, interspersed with woodlands along the floodplain and within the lowlands of small drainages and ravines (U.S. Army 1994*). Major grasses include big bluestem (*Andropogon gerardii*), indian grass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), little bluestem (*Scizachyrium scoparium*), and sideoats gramma (*Bouteloua curtipendula*) (U.S. Army 1994*). Woodlands within the small stream valleys and ravines are dominated by bur oak (*Quercus macrocarpa*), chinkapin oak (*Quercus muhlenbergii*), American elm (*Ulmus americana*), red mulberry (*Morus rubra*), bitternut hickory (*Carya cordiformis*), black walnut (*Juglans nigra*), green ash (*Fraxinus pennsylvanica*), hackberry (*Celtis occidentalis*), and honey locust (*Gleditsia triacanthos*–U.S. Army 1994*).

Fort Riley has a temperate continental climate characterized by hot summers, cold, dry winters, moderate

winds, low humidity and a pronounced peak in rainfall late in the spring and in the first half of summer (U.S. Army 1994*). Mean daily high temperatures in January and July are 4.2°C and 33.7°C, respectively. Mean daily low temperatures in January and July are -7.8°C and 19.5°C, respectively. Mean annual precipitation is 80.4 cm and ranges from 40.6 cm to 142.2 cm (U.S. Army 1994*).

Fort Riley has been opened to public hunting since 1982, although trapping is prohibited. Hunters must check in on a daily basis and report all animals harvested. Raccoons are not frequently harvested on Fort Riley, and no harvests were reported from 1995 to 1998.

Methods and Materials

We captured Raccoons during 4 periods: October-December 1995, January-April 1996, October-November 1996, and March-June 1997. We captured Raccoons in wire box traps baited with sardines and checked daily. We set traps in a 250-ha area in the southern region of Fort Riley to increase the likelihood that study animals would overlap in space and resource use. We immobilized Raccoons with an intramuscular injection of ketamine hydrochloride and acepromazine (10:1 ratio, dosage = 0.2 ml/kg). Our capture and handling protocol, no. 1098, was approved by the Institution Animal Use and Care Committee at Kansas State University. We recorded the following data for all captured Raccoons: body mass, body length, tail length, ear length, hindfoot length, shoulder height, sex, reproductive condition, age class, ear tag number, injuries, and ectoparasite load. Body mass was compared between sexes using t-tests (SAS Institute 1985). At time of capture, male Raccoons were aged according to body size and toothwear (Grau et al. 1970), and for females, size and pigmentation of teats (Kaufmann 1982). Raccoons were considered adult if they were > 1.5 year old at time of capture, whereas all other raccoons were considered juveniles. Forty-four Raccoons were captured 61 times, including 5 adult males, 9 adult females, 13 juvenile males, and 17 juvenile females. Radio-transmitter collars (Advanced Telemetry Systems, Inc., Isanti, Minnesota 55040) were placed on all adults captured (5 males, 9 females) for this study. Due to early deaths, 2 Raccoons (1 male, 1 female) were not monitored long enough to be used in analyses.

We analyzed radio-telemetry data in two seasons defined as summer (April-September) and winter (October-March). The two seasons were defined in this way to parallel major changes in climate and animal responses to climatic change. Our delineations of two climatic seasons encompassed several phases of the raccoon reproductive cycle (Kaufmann 1982); however, climatic influences on raccoon movements likely obscure reproductive influences (Schneider et al. 1971), especially in higher latitudes where seasonal differences are more pronounced.

We recorded telemetry locations for each raccoon 1-2 times per week and > 12 hours apart, which we considered sufficient to establish independence (White and Garrott 1990). We radio-tracked Raccoons simultaneously from two vehicles using null-peak systems which consisted of dual, four-element Yagi antennas. We conducted radio-tracking primarily during 1800-0900 hours, when Raccoons were likely to be most active (Kaufmann 1982; Sanderson 1987). We calculated location estimates using the maximum likelihood estimation option in the program Locate II (Pacer, Inc., Truro, Nova Scotia). Mean error for reference collars (known locations) was 65 m (95% of errors were ≤ 166 m).

We calculated seasonal and annual sizes of home ranges of Raccoons using the 95% minimum convex polygon method (Mohr 1947), as calculated by CALHOME (Kie et al. 1994). We calculated annual home ranges for Raccoons with > 50 locations (mean ± SD = 60 ± 6) and ≥ 10 months of radio-tracking. Area observation curves (Odum and Kuenzler 1955) showed that 21-24 locations were needed to effectively determine seasonal home ranges for individual Raccoons. Therefore, we calculated seasonal home ranges for Raccoons with > 25 locations (29 ± 3) and > 3 months of radio-tracking per season. Seasonal home ranges during summer were pooled across years. We compared seasonal and sexual differences in home range sizes using 2-tailed t-tests (SAS Institute 1985).

Habitat types were delineated using geographic information system (GIS) data provided by the Conservation Division at Fort Riley. Habitat types on Fort Riley were classified at 2 m resolution as grassland, woodland, built areas, water or sandy areas (Lauver et al. 1996*). Grassland was defined as all pasture (hayfield), rangeland, and other herbaceous cover having insufficient trees and/or shrubs to be classified as "woodland." Woodland was defined as wooded areas with > 15% canopy closure. Built areas were defined as areas of intensive use with much of the land covered by structures. Water included all water bodies larger than the minimum mapping unit of 2 m. Sandy areas were defined as river sand bars, rock quarries, sand and gravel pits and other permanently exposed ground (Lauver et al. 1996*). The placement of land cover boundaries had a spatial accuracy of ±10 m (Lauver et al. 1996*). Total coverage of these habitat types on Fort Riley was 82% grasslands, 16% woodlands, 2% built areas, and a trace of both water and sandy areas. Total coverage of the 250-ha trapping area consisted of 62% grasslands, 37% woodlands, and 1% built areas.

We determined habitat use and availability for each raccoon using the computer program ArcView GIS (Version 3.0, Environmental Systems Research Institute, Inc., Redlands, California 92373). We calculated selection indices by dividing observed numbers of locations by expected numbers of locations for each habitat type. We calculated the expected number of

locations for each habitat type as the total number of locations inside the home range multiplied by the proportion of home range consisting of that habitat (Kamler 1998). A habitat selection index > 1 indicates greater than expected use for that habitat type; an index < 1 indicates less than expected use for that habitat type. We used log-transformed selection indices (Zar 1984) and 2-tailed t-tests to compare habitat selections between seasons and between sexes. We used only selection indices for grassland habitat to determine statistical differences because it was the most dominant habitat type in the study area, and analyses of other habitat types would not have been independent (Kamler 1998).

Results

Three Raccoons (females) were monitored from April to September 1996, and 9 Raccoons (5 females, 4 males) were monitored from April 1997 to March 1998. Annual and seasonal home ranges of male Raccoons were larger than those of females ($P < 0.05$). Home range size (mean ± SE) in summer was 244 ± 26 ha (n = 4) for males, and 103 ± 10 ha (n = 8) for females. The home range size in winter was 193 ± 11 ha (n = 4) for males, and 52 ± 12 ha (n = 4) for females. Annual home range of male Raccoons, 266 ± 14 ha (n = 4), was more than twice as large as that of females, 122 ± 52 ha (n = 4). Home ranges of female Raccoons decreased ($P < 0.05$) by 50% from summer to winter, whereas home ranges of males decreased ($P < 0.05$) by 21% from summer to winter. Home ranges of females raccoons overlapped extensively, whereas home ranges of males were exclusive (Figure 1). A fifth adult male that died before relevant data were collected had a capture and death location outside the home range boundary of the other adult males (Figure 1). The mass (mean ± SE) of males (9.1 ± 0.6 kg) was larger ($P < 0.05$) than that of females (7.0 ± 0.4 kg).

Both male and female Raccoons generally selected grasslands less than expected, and woodlands more than expected (Table 1). Habitat selection of females differed ($P < 0.05$) between seasons, as selection of grassland habitats decreased from summer (0.90) to winter (0.49) (Table 1). Habitat selections of males did not differ ($P = 0.22$) between summer (0.64) and winter (0.84) (Table 1). Female Raccoons selected more ($P < 0.05$) grassland habitats than males during summer, whereas males selected more ($P < 0.05$) grassland habitats than females during winter (Table 1). Habitat selection indices of Raccoons were relatively consistent within sexes despite availability of grassland habitat in individual home ranges varying from 31-83% in summer and 16-77% in winter.

Discussion

Although male Raccoons are larger than females, the large size of male home ranges cannot be explained by energetic requirements alone (Gehrt and Fritzell 1997). The larger home ranges of male Raccoons are likely a result of different behavioral tactics employed by male and female Raccoons (Sandell 1989; Gehrt and Fritzell 1997, 1998). Females rear young by themselves, so their movements and home range sizes are closely related to energetic demands and available resources (Sandell 1989; Gehrt and Fritzell 1997, 1998). In contrast, males are polygynous and free of raising young, so their movements and home range sizes are more closely related to access and distribution of females (Sandell 1989; Gehrt and Fritzell 1997, 1998).

Seasonal fluctuations in mean home range sizes of Raccoons were not observed in the southern United States (Gehrt and Fritzell 1997), but were observed in more northern areas (Schneider et al. 1971; Glueck et al. 1988). The reductions in home range sizes from summer to winter in this study were likely the result of reduced activity of Raccoons in winter (Schneider et al. 1971; Glueck et al. 1988). Raccoons are known to lose weight during winter after a fat build-up during summer and early fall (Mech et al. 1968; Johnson 1970; Moore and Kennedy 1985; Zeveloff and Doerr 1985). They may reduce activity and forage less in winter because they can rely more on fat for their ener-

TABLE 1. Habitat selection indices[a] of adult Raccoons monitored on Fort Riley Military Reservation, Kansas, April 1996 to March 1998.

Season	Sex	n	Grassland		Woodland	
			Mean ± SE	Range	Mean ± SE	Range
Summer	female	8	0.90 ± 0.08	0.60-1.30	1.16 ± 0.12	0.72-1.68
	male	4	0.64 ± 0.06	0.55-0.82	1.58 ± 0.23	1.20-2.19
Winter	female	4[b]	0.49 ± 0.07	0.37-0.69	1.63 ± 0.27	1.12-2.13
	male	4	0.84 ± 0.15	0.65-1.29	1.42 ± 0.32	0.91-2.36

[a]Habitat selection indices were calculated by dividing the percentage of that habitat type used by the percentage of that habitat type available. Habitat selection indices > 1 indicate greater than expected use, and indices < 1 indicate less than expected use.

[b]Four females were not monitored long enough (>3 months) during winter for habitat analyses.

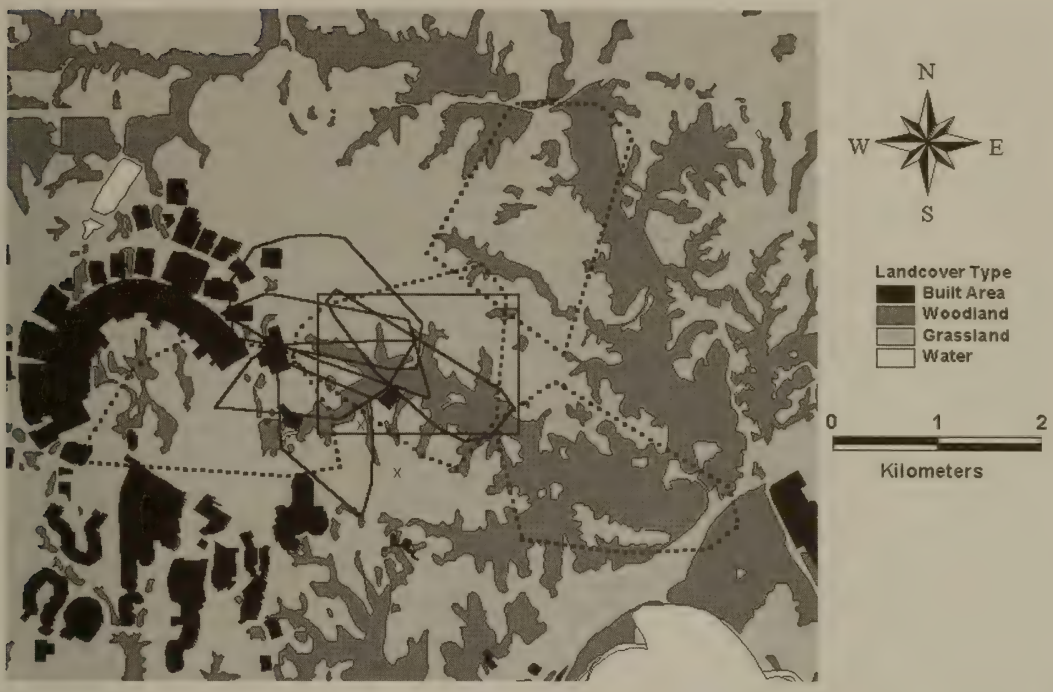


FIGURE 1. Summer home ranges of adult Raccoons monitored in 1997 on Fort Riley Military Reservation, Kansas (similar patterns were observed in other seasons and years). Solid polygons represent females ($n = 5$), whereas dashed polygons represent males ($n = 4$). The "X" represents the capture and death locations, of another adult male that died before relevant data were collected. Solid rectangle represents 250-ha trapping area.

getic demands. Foraging in winter may also be more energetically demanding than in summer because of the decrease in ambient temperature and reductions in food resources. A majority of Raccoon diets, including fruits, nuts, invertebrates, and small aquatic and terrestrial vertebrates (Kaufmann 1982; Smith et al. 1987), are reduced in abundance or absent during winter in temperate regions.

In winter, male Raccoons had a smaller reduction in home range than did females. This may have been due to home range maintenance by male Raccoons. When males are polygynous and have exclusive home ranges, competition over access to areas with many females probably goes on for most of the year (Sandell 1989). Therefore, males that have acquired home ranges should show their presence there throughout the year because it is easier to maintain an exclusive home range than to establish one (Sandell 1989). Additionally, reproductive activities can influence home range sizes of solitary carnivores (Sandell 1989), including Raccoons (Fritzell 1978b). Because winter includes the breeding period for Raccoons in Kansas (Bee et al. 1981), male Raccoons could have maintained larger home ranges than females due to inreased movements related to breeding activities (Seidensticker et al. 1988).

On our study site, home ranges of adult females overlapped extensively, whereas home ranges of adult males were exclusive (Figure 1). Non-overlapping home ranges of male Raccoons may have been a result of a small sample; however, previous studies showed that although home ranges of females overlapped throughout their range, home ranges of males may or may not overlap (Fritzell 1978a; Lehman 1984; Seidensticker et al. 1988; Gehrt and Fritzell 1997). Reasons for variability in home range overlap of male Raccoons may be related to both the degree of human exploitation, and social status of males that were monitored. For example, degree of human exploitation can contribute to variability in social organizations of carnivores (Crabtree and Sheldon 1999), so unexploited populations likely exhibit more stable social organizations than exploited ones. Additionally, previous research from unexploited populations of Raccoons showed that although home ranges of subordinate males overlapped, the home ranges of the most dominant males did not overlap (Gehrt and Fritzell 1997, 1999). Because dominance of male Raccoons is positively related to size (Gehrt and Fritzell 1999), the home ranges of the largest males may not overlap. The five males (including the male that had an early death) monitored in our study were the largest (8-11

kg) captured in 2.5 years of trapping, suggesting that they were the most dominant males in our study site. Thirteen juvenile males were also captured during the study, suggesting that home ranges of more numerous younger males likely overlapped those of large adult males.

Habitat selections differed between males and females in both seasons, possibly as a result of energetic differences between the sexes. In summer, females may have selected more grasslands than males due to differences in energetic requirements as a result of rearing young. Previous studies also found intersexual differences in habitat use of Raccoons, especially during the rearing season (Fritzell 1978b; Sherfy and Chapman 1980; Endres and Smith 1993). Sexual differences in habitat use by Raccoons may have also resulted from sexual dimorphism, which can lead to sexual segregation in habitat use and niche partitioning (Selander 1966; Moors 1980).

In winter, females selected less grassland and more woodland than males. Woodlands contain tree cavities that provide cover and protection from predators, especially as females decrease movements and become less active as a result of pregnancy (Endres and Smith 1993). During our study, three female Raccoons died from predation during winter and early spring, suggesting that females were more vulnerable to predation during this period (Kamler 1998). Seasonal differences in habitat use by males did not differ, probably as a result of their continuous home range maintenance. Females likely exhibit greater fluctuations in energetic requirements, and consequently greater variability in habitat use, as they rear young during summer, but become less active and pregnant during winter. Thus, the evolutionary and behavioral factors that contribute to intersexual differences in raccoon home range sizes also likely contributed to intersexual differences in their habitat selections.

Acknowledgments

We thank D. Jones, H. Abel, M. Pont, Carin Richardson and other personnel at the Conservation Division on Fort Riley for their assistance. We also thank J. Beckman, B. Bowman, J. Boyer, M. Dryden, J. Goheen, D. Hogan, B. Kamler, D. Martin, C. Perchellet, T. Snyder, Chad Richardson, and G. Truan for assistance with field work and other aspects of the project. We thank K. Kauhala and other reviewers for helpful comments on this paper. This project was funded by the Department of Defense, in cooperation with the Kansas Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, and Kansas State University.

Documents Cited (marked * in text)

Lauver, C. L., W. H. Busby, K. Kindscher, and **J. L. Whistler**. 1996. Identification and delineation of loggerhead shrike habitat on the Fort Riley Military Reservation. Kansas Biological Survey Report 69. 29 pages.

U. S. Army. 1994. Integrated natural resource management plan for Fort Riley, Kansas. Louis Berger and Associates, Inc., Washington, D.C. 161 pages.

Literature Cited

Bee, J. W., G. E. Glass, R. S. Hoffmann, and **R. R. Patterson**. 1981. Mammals in Kansas. University of Kansas Printing Service, Lawrence, Kansas. 300 pages.

Crabtree, R. L., and **J. W. Sheldon**. 1999. Coyotes and canid coexistence in Yellowstone. Pages 127-163 *in* Carnivores in ecosystems: the Yellowstone experience. *Edited by* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva. Yale University Press, New Haven, Connecticut.

Endres, K. M., and **W. P. Smith**. 1993. Influence of age, sex, season and availability on den selection by raccoons within the central basin of Tennessee. American Midland Naturalist 129: 116-131.

Fritzell, E. K. 1978a. Aspects of raccoon (*Procyon lotor*) social organization. Canadian Journal of Zoology 56: 260-271.

Fritzell, E. K. 1978b. Habitat use by prairie raccoons during the waterfowl breeding season. Journal of Wildlife Management 42: 118-127.

Gehrt, S. D., and **E. K. Fritzell**. 1997. Sexual differences in home ranges of raccoons. Journal of Mammalogy 78: 921-931.

Gehrt, S. D., and **E. K. Fritzell**. 1998. Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. Animal Behaviour 55: 1211-1227.

Gehrt, S. D., and **E. K. Fritzell**. 1999. Behavioral aspects of the raccoon mating system: determinants of consortship success. Animal Behaviour 57: 593-601.

Glueck, T. F., W. R. Clark, and **R. D. Andrews**. 1988. Raccoon movement and habitat use during the fur harvest season. Wildlife Society Bulletin 16: 6-11.

Grau, G. A., G. C. Sanderson, and **J. P. Rogers.** 1970. Age determination of raccoons. Journal of Wildlife Management 34: 364-372.

Johnson, A. S. 1970. Biology of the raccoon in Alabama. Alabama Agricultural Experiment Station Bulletin 402: 1-148.

Kamler, J. F. 1998. Ecology and interspecific relationships of mammalian predators on Fort Riley Military Reservation, Kansas. M.S. thesis. Kansas State University, Manhattan. 150 pages.

Kaufmann, J. H. 1982. Raccoon and allies. Pages 567-585 *in* Wild mammals of North America. *Edited by* J. A. Chapman and G. A. Feldhamer. The John Hopkins University Press, Baltimore, Maryland.

Kie, J. G., J. A. Baldwin, and **C. J. Evans**. 1994. CALHOME: home range analysis program. U.S. Forest Service, Pacific Southwest Research Station, Fresno, California. 19 pages.

Lehman, L. E. 1984. Raccoon density, home range, and habitat use on south-central Indiana farmland. Indiana Department of Natural Resources P-R Bulletin 15: 1-66.

Mech, L. D., D. M. Barnes, and **J. R. Tester**. 1968. Seasonal weight changes, mortality, and population structure of raccoons in Minnesota. Journal of Mammalogy 49: 63-73.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37: 223-249.

Moore, D. W., and **M. L. Kennedy**. 1985. Weight changes and population structure of raccoons in western Tennessee. Journal of Wildlife Management 49: 906-909.

Moors, P. J. 1980. Sexual dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. Oikos 34: 147-158.

Odum, E. P., and **E. J. Kuenzler**. 1955. Measurement of territory and home range size in birds. Auk 72: 128-137.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164-182 *in* Carnivore behavior, ecology, and evolution. *Edited by* J. L. Gittleman. Cornell University Press, Ithaca, New York.

Sanderson, G. C. 1987. Raccoon. Pages 486-499 *in* Wild Furbearer Management and Conservation in North America. *Edited by* M. J. Novak, J. A. Baker, M. E. Obbard, and B. Malloch. Ministry of Natural Resources, Ontario.

SAS Institute. 1985. SAS user's guide: statistics, 5th edition. SAS Institute, Inc., Cary, North Carolina. 956 pages.

Schneider, D. G., L. D. Mech, and **J. R. Tester**. 1971. Movements of female raccoons and their young as determined by radio-tracking. Animal Behaviour Monographs 4: 1-43.

Seidensticker, J., A. J. T. Johnsingh, R. Ross, G. Sanders, and **M. B. Webb**. 1988. Raccoons and rabies in Appalachian Mountain Hollows. National Geographic Research 4: 359-370.

Selander, R. K. 1966. Sexual size dimorphism and differential niche utilization in birds. Condor 68: 113-151.

Sherfy, F. C., and **J. A. Chapman**. 1980. Seasonal home range and habitat utilization of raccoons in Maryland. Carnivore 3: 8-18.

Smith, R. A., M. L. Kennedy, and **G. D. Baumgardner**. 1987. Food habits of the raccoon (*Procyon lotor*) at Land Between the Lakes. Journal of the Tennessee Academy of Science 62: 79-82.

White, G. C., and **R. A. Garrott.** 1990. Analysis of radio-tracking data. Academic Press, Inc., San Diego, California. 383 pages.

Zar, J. H. 1984. Biostatistical analysis, 2nd edition. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 718 pages.

Zeveloff, S. I., and **P. D. Doerr**. 1985. Seasonal weight changes in Raccoons (Carnivora: Procyonidae) of North Carolina. Brimleyana 11: 63-67.

Received 4 April 2001
Accepted 25 November 2003

Sandhill Crane, *Grus canadensis*, Nesting in the Yorkton Wetland Complex, Saskatchewan

Ann M. Burke

International Crane Foundation, E-11376 Shady Lane Road, Baraboo, Wisconsin 53913, USA

Burke, Ann M. 2003. Sandhill Crane, *Grus canadensis*, nesting in the Yorkton wetland complex, Saskatchewan. Canadian Field Naturalist 117(2): 224-229.

Surveys for Sandhill Cranes (*Grus canadensis)* were conducted near Yorkton, Saskatchewan during the summers of 1995, 1996 and 1997. Seven nesting territories were identified and habitat measurements were taken at six nests. All nests were located in the emergent deep marsh zone of open water marshes within residual stands of Hardstem Bulrush (*Scirpus acutus)*. Seven eggs were measured in four nests. Estimated hatching dates ranged from 20 May to 9 June. Total productivity for the three years was 0.80 chick per breeding pair (12 offspring fledged by 15 pairs). Individual pair productivity was impacted by disturbance, mate change, adult mortality, and predation. Hunting mortality may also impact the population.

Key Words: Sandhill Crane, *Grus canadensis*, reproduction, productivity, aspen parkland, crane hunting, Saskatchewan.

In 1993, the [Canadian] National Recovery Plan for the Whooping Crane recommended that "preliminary field studies be conducted to determine migration, staging, and wintering range for resident Sandhill Cranes" (Edwards et al. 1994). Resident Sandhill Crane (*Grus canadensis*) population parameters have, in part, been used to evaluate potential reintroduction sites for the Whooping Crane (*Grus americana*) (Drewien 1973; Bishop 1988; McMillen 1988; Nesbitt 1988*; McMillen et al. 1992) because the Whooping Crane is absent from large portions of its historic range. Establishment of additional Whooping Crane populations reduces the likelihood the species could become extinct in the wild.

In 1994, the Canadian Wildlife Service (CWS) identified and assessed approximately 40 potential reintroduction sites located within the historic range of the Whooping Crane (Lyon et al. 1995*). Three wetland complexes appeared to contain adequate Whooping Crane habitat: (1) the Overflowing River Area (Leaf Lake) in northwestern Manitoba, (2) the Saskatchewan River Delta in northeastern Saskatchewan, and (3) the Yorkton Wetland Complex (YWC) in southeastern Saskatchewan. The YWC was selected for further study due to the presence of Sandhill Cranes, the ability of Ducks Unlimited Canada to manipulate water levels, its size and accessibility, and because its location within the aspen parkland ecotone was thought to have been optimal breeding habitat for the Whooping Crane historically (Lyon et al. 1995*).

Cranes in the study area are referred to as mid-continent Sandhill Cranes as they migrate through the Great Plains of North America (Central Flyway) and winter primarily in Oklahoma, Texas, New Mexico and Mexico (Tacha et al. 1984). This paper describes Sandhill Crane eggs and nests, the habitat surrounding nest sites, and pair productivity within the YWC.

Study Area and Methods

The study area is located in southeastern Saskatchewan in the Aspen Parkland (Bird 1961). The aspen parkland is a zone of transition between the boreal forest to the north and mixed-grass prairie to the south (Rowe 1987). Under pristine conditions, parkland is differentiated from grasslands by the presence of more than 15% tree cover (Strong and Leggat 1981). Prominent wetlands include fresh and variably saline marshes and semi-permanent shallow ponds bordered by emergents, shrubs, and trees (National Wetlands Working Group 1988).

The principal study area (approximately 736 km^2) encompassed the YWC and Rokeby Marsh located to the south and west of Yorkton, Saskatchewan. The YWC comprises 10 major basins that are linked through a series of water control structures. Total basin size is 3394 ha. Rokeby Marsh supports the largest number of resident Sandhill Cranes and was selected as the main study site. Rokeby Marsh (790 ha) is located approximately 17 km southeast of Yorkton, and 8 km west of Saltcoats. Lands within the YWC are predominantly privately owned.

Efforts to locate Sandhill Crane pairs were conducted from 28 May – 20 August 1995, 28 April – 20 August 1996, and 1 May – 25 July 1997. Surveys to locate cranes were conducted daily from 05:00-07:00 h and 18:00-20:00 h from a vehicle on roads external to the marshes, on foot in uplands adjacent to wetland areas, or from a canoe on open water. Landowner permission was obtained before entering private property. Systematic auditory censuses (Bennett 1978) were conducted using a taped recording of Sandhill Crane unison, guard, and flight calls. Calls were broadcast at 15- 25 minute intervals with a battery operated Burnham Brothers™ model TS-12W Predator Call. After playing the tape,

the observer noted responding crane vocalizations and bearing, and scanned the area using a spotting scope and binoculars. After 15 minutes, the observer moved approximately 0.4 km to repeat the broadcast.

During surveys, the following data were recorded: location (township, section, range), number of cranes, age (juvenile or adult based on cheek patch color and feather coloration on head and neck) (Tacha 1988), sex (determined if a bird was observed unison calling, Archibald 1976), behavior, movements, habitat type, and the presence/absence of feather painting (Johnsgard 1983). (After digging in the mud and debris, adult and juvenile Sandhill Cranes preen the material over most of the body feathers, thus producing a stain that is usually a bright rusty brown (Walkinshaw 1973; Lewis 1979). Such feather painting is especially characteristic of adult cranes on nesting territories (Johnsgard 1983)). Wetland type was recorded based on Millar's (1976) classification system for aspen parkland wetlands.

Paired cranes were recorded as breeders or non-breeders. Due to the absence of marked individuals, I used behavior and repeated observations of pairs/families, in specific locations, to identify nesting territories. Pairs engaging in territorial defense, incubating eggs, or seen with young were identified as breeding pairs.

Nests were located by visual observation of incubating birds or when birds exchanged incubation duties. To reduce disturbance and thus the likelihood of abandonment, nest sites were visited only during the later stages of incubation. GPS readings were taken at each nest. Eggs were measured, weighed, and aged (estimated) using the flotation method as described by Fisher and Swengel (1991). Nests and eggs were photographed. Nest diameter, height above water, and water depths at 1 m and 2 m intervals in each cardinal direction were measured.

Once the nest was no longer in use, we recorded species composition within a 5 m radius of each nest using the Daubenmire canopy coverage method of vegetation analysis (Daubenmire 1959). Vegetative composition of the nest was recorded and visual obstruction measurements (a reliable measure of the height and density of vegetation) were determined at 5 m increments up to 20 m in each cardinal direction from the nest using a Robel pole (Robel et al. 1970). Distances to specific habitat features (e.g., nearest fence, woody vegetation, road, residence and upland) were determined by pacing or by measurement from aerial photographs. Pairs with young were located tri-weekly to determine survival rates and monitor habitat use.

Results

Sandhill Cranes arrived on the YWC in late March and early April each year of the study. I located seven nesting pairs within the YWC, five on Rokeby Marsh, one on Leech Lake, and one on Maddaford Marsh. The auditory census technique elicited a vocal response from cranes an average of 41% of the time.

In 1996-1997, five of seven nest sites were evaluated on Rokeby Marsh. Nesting began in late April – early May and ended in early June. All nests were located in the emergent deep marsh zone of open water marshes

TABLE 1. Data on Sandhill Crane eggs (n=7) from nests in Rokeby Marsh, Saskatchewan, May – June 1996 and 1997.

Nest	Date measured	Egg weight (g)	Egg Length (cm)	Egg Width (cm)	Estimated Egg weight at laying[a] (g)	Estimated age (days)[b]	Estimated hatch date
1	11 May 1996	172 158	9.8 10.7	6.0 5.8	193 170	22-23 19-21	20-28 May
2	26 May 1996	192 180	10.5 9.9	6.1 6.0	213 194	18-21 18-21	9-11 June
3	28 May 1996	128 122	8.8 8.6	5.5 5.3	145 132	21-25 18-21	Did not hatch
4	3 June 1996	– –	– –	– –	– –		1-2 June
5	28 May 1997	123	8.1	5.6	139	27-28	29-31 May

[a] Fresh egg weight was estimated in grams by the formula $F_w = (0.546) \times [\text{width}^2 (\text{cm}) \times \text{length (cm)}]$ (Fisher and Swengel 1991).

[b] Estimation based on flotation technique as described by S. Swengel. Unpublished data. General guidelines for estimating the age of Sandhill crane eggs. International Crane Foundation, Baraboo, Wisconsin.

an average of 40 m (r = 14-54 m) from the nearest upland. Nests were composed entirely of Hardstem Bulrush (*Scirpus acutus*) and located in residual stands of Hardstem Bulrush. Visual obstruction measurements, 1, 5, 10 and 20 m from each nest averaged 68 cm, 49 cm, 56 cm, and 51 cm, respectively. Average visual obstruction measurements 1 m from crane nests were greater or equal to those taken 5 m from the nest. Nests were located in an average of 26 cm (r = 13-48 cm) of water, averaged 37 cm (r = 27-55 cm) in height, and alternative nest starts (between two and seven) were discovered within 100 m of each nest (Tacha et al. 1992).

Distance measures to habitat features varied greatly. Nests were 333–1800 m from a gravel road, 23–381 m from woody vegetation, 20–650 m from a barbed-wire fence, and 1.1–2.1 km from a residential building.

Seven eggs were measured in four nests (Table 1). Estimated hatching dates ranged from 20 May – 9 June. No re-nesting attempts were observed by failed pairs and pair productivity varied by year (Table 2). Total productivity for the three years was 0.80 fledged chicks per pair (15 pairs fledged 12 offspring).

Individual pair productivity was affected by disturbance, mate change, and adult mortality. In 1996, two days before the first egg of the clutch was estimated to hatch on Territory 1, cattle trampled the vegetation extensively around the nest and created deep channels in the water <1 m from the pairs' nest. Three days later, the pair and one chick abandoned the nest site. In 1996, I visited the nest in Territory 3 after an estimated 18-21 days of incubation. The pair abandoned the nest within 2 days but remained on the territory until early July. As no egg remains were found in the nest, a Coyote (*Canis latrans)* probably destroyed the clutch based on Stern et al. (1987) observations of crane nest predation. This territory was unoccupied in 1997.

In 1995 and 1996, the pair on Territory 2 was highly territorial, successfully fledging offspring, and was feather painted. The pair copulated successfully on 7 May 1996. In 1997, however, the female did not have feather painting and on three occasions did not respond to the male's pre-copulatory parade or calls. On five occasions, the pair flew across the marsh in the early morning to spend the day feeding with a flock of 130 Sandhill Cranes, Snow Geese (*Chen caerulescens*) and

TABLE 2. Productivity of Sandhill Crane pairs (n=7) on Rokeby Marsh and the Yorkton Wetland Complex, 1995-1997, Saskatchewan, Canada.

Territory Number	Territory Location	Year	Number of Eggs	Number of Fledged Young
1	South end of Rokeby Marsh	1995	?[a]	0
		1996	2	1[c]
		1997	2	2
2	Southwest side Rokeby Marsh	1995	?[a]	1
		1996	2	1
		1997	Did not nest	0
3	Northwest side Rokeby Marsh	1995	Pair absent	–
		1996	2	0[b]
		1997	Pair absent	–
4	East side Rokeby Marsh	1995	?[a]	1
		1996	2	1
		1997	Pair absent	–
5	Northeast side Rokeby Marsh	1995	?[a]	1
		1996	?[a]	2
		1997	1	0[b]
6	Southeast side Maddaford Marsh	1995	?[a]	0[b]
		1996	Pair present	Unknown
		1997	Pair present	Unknown
7	West side Leech Lake	1995	?[a]	1
		1996	?[a]	0[b]
		1997	?[a]	1[c]

[a] Nest not located
[b] Pair observed with pre-fledged chick
c Pair observed with two pre-fledged chicks

Canada Geese (*Branta canadensis*). The pair remained on the territory until late July but did not initiate nesting. These behavioral changes suggest that a different female occupied the territory in 1997 than in the previous two years.

On 3 June 1996, the pair on Territory 4 was observed with two newly hatched chicks. On 14 and 20 July, only a single adult with one chick was observed. On 28 July, a lone fledged juvenile (presumably abandoned by its widowed parent) was seen on the territory. In 1997, cranes were absent from this territory.

All nesting cranes were feather painted. During incubation and early chick rearing in May and June, four breeding adults were in partial molt of primary and secondary feathers. Pairs with fledged chicks remained on territories until mid-to-late August in all years.

Discussion

Sandhill Crane pairs are highly territorial during the breeding season and return each year to the same territory. An undisturbed nest site associated with water is a critical habitat component for Sandhill Cranes and nests are usually constructed using residual vegetation from the previous growing season (Armbruster 1987). Sandhill Cranes may prefer to nest in tall, emergent vegetation (with adequate water depth) because it provides cover during early spring (Provost et al. 1992). Crane productivity is greater in areas where wetlands are bordered by agricultural lands (Meine and Archibald 1996). These factors serve to explain why since the early 1900s, Rokeby Marsh has traditionally supported higher crane nesting densities than other wetlands within the YWC (Houston 1949; Reed 1903).

Historically, Rokeby Marsh has had less human disturbance than other marshes in the YWC and has maintained its vegetative composition of dense Hardstem Bulrush. Rokeby Marsh has the most stable, permanent water levels of any of the wetlands in the YWC and a mosaic of grazed and harvested pastures, fallow areas, and cultivated lands surrounds it. During dry years, water levels on Rokeby Marsh are low, but the marsh has never dried out completely (R. Kirkness, Ducks Unlimited Canada, personal communication). Permanent wetlands retain their character for decades except in years of extreme drought (Eldridge 1990). Under permanent water conditions, Hardstem Bulrush is stable and may survive for many years (Millar 1976).

In other wetlands within the YWC, shorelines and water depths fluctuate more widely, and vary in vegetative structure and diversity (Schmidt 1973*). During the recent study, new growth was sparse along many basin shorelines and residual emergent vegetative growth was virtually non-existent when cranes were initiating nesting in early spring.

Sandhill Crane pairs are capable of producing at most two offspring per year. Year-to-year variation in the number of offspring reared produces significant variation in annual productivity (Johnsgard 1983). The number of young fledged per year was 0.80 young fledged per pair over three years (15 pairs, 12 young), above the norm of 0.35 young per year cited by Nesbitt (1992). In contrast, Dimatteo (1992), in aspen parkland habitat on the Agassiz National Wildlife Refuge in northwestern Minnesota found 1.2 young fledged per pair during a two-year period (34 pairs, 42 young). However, nesting and fledging success rates depend largely upon local and highly variable factors such as weather conditions, water levels, degree of disturbance, and predation rates (Johnsgard 1983).

In my study, disturbance, mate change and adult mortality affected individual pair productivity. Indirect evidence indicated that predation also impacted productivity. We frequently observed Coyotes in uplands adjacent to wetland areas, and I observed American Crows (*Corvus brachyrhynchos)* destroying Blue-winged Teal (*Anas discors)* nests. On one occasion, a Coyote repeatedly flushed an adult crane in an upland adjacent to Rokeby Marsh, and a Coyote flushed a female Sharp-tailed Grouse (*Tympanuchus phasianellus)* and ate five pre-fledged chicks. Depredated duck carcasses were not uncommon in the shallow marsh zones around Rokeby and Maddaford Marsh and the wetlands used by roosting cranes. Coyote predation was found to be the major mortality factor affecting eggs and pre-fledged Sandhill Crane chicks in Oregon (Stern et al. 1987; Littlefield and Lindstedt 1992). Other possible crane predators in the complex include: Common Ravens (*Corvus corax)*, Raccoons (*Procyon lotor)*, Striped Skunks (*Mephitis mephitis*), Red Foxes (*Vulpes vulpes*), Mink (*Mustela vison*), Northern Harriers (*Circus cyaneus*), and Great Horned Owls (*Bubo virginianus)* (Schmidt 1973*; Genter 1985; Armbruster 1987).

I found between three (1997) and five (1995) territories occupied by cranes on Rokeby Marsh. Historical records indicate that in 1901-1964 and 1993, Rokeby Marsh has supported one to six nesting pairs of Sandhill Cranes annually (Houston 1949; Reed 1903; D. Hjertaas, Saskatchewan Environment and Resource Management, personal communication). This evidence suggests inter-year variation in carrying capacity. Climatic conditions, water levels, vegetative structure, and the size or characteristics of uplands within territories vary irregularly over time and alter habitat conditions, resulting in a fluctuating number of crane pairs on the marsh within any given year. Variation in nesting conditions and short breeding season length combine to limit habitat carrying capacity.

Historical records indicate that although Sandhill Cranes have occurred in the Yorkton region for over 120 years, the number of resident breeding pairs has declined sharply. During the late 1880s – 1890s, Sandhill Cranes were recorded as regular and common breeders around Rokeby Marsh, Good Spirit Lake, and Crescent Lake but by 1949, cranes were listed as only rare summer residents in the Yorkton area (Houston

1949). Loss and degradation of wetland and wildlife habitat, drought, and sport and subsistence hunting likely impacted these historic resident crane populations (Schmidt 1973*, Johnson 1976; Turner et al. 1987).

We found low annual productivity and concurrent low recruitment rates (percentage of juveniles within the population) on Rokeby Marsh and the YWC. This may explain why previously occupied territories are vacant in some years. Offspring return to their natal area as subadults and, as adults, eventually select mates and either colonize new territories in the area or replace absent pairs (Drewien 1973; Duan et al. 1997). Vacant territories may be a consequence of low recruitment and survival rates as there are limited numbers of resident adults available to fill vacant yet suitable territories. Low annual recruitment rates limit the ability of Sandhill Cranes to recover from population declines (Tacha et al. 1992).

Hunting mortality may also limit the growth of the resident crane population. Resident cranes are exposed to hunting along their entire migratory route. Timing of their departure from the study area and from traditional staging areas may expose this population to greater hunting pressure than on cranes from other breeding populations. To date, no long term data on recruitment or survival rates have been collected for the mid-continental populations, and currently the effects of hunting on specific breeding populations are unknown (Drewien et al. 1995). Banding recoveries indicate that hunting mortality in the mid-continental flock can equal or exceed the species estimated 10% recruitment rate (Johnsgard 1983). A future investigation to determine the effect hunting plays on resident crane populations in southern Saskatchewan is warranted.

Acknowledgments

Project funding was provided by Conoco Inc., Gulf Coast Region, Mr. William Lishman and the Migration Foundation, and the Calgary Zoological Society. Ducks Unlimited Canada, Honda Canada, Brian Johns (CWS), and Dale Hjertaas (Saskatchewan Environment and Resource Management) supplied logistical support.

I extend thanks to George Archibald (International Crane Foundation), Rob Kirkness (Ducks Unlimited Canada), and James Hardin (University of Wisconsin – Stevens Point) and to my field assistants, Dan Golner, Isabel Ritchie, and William Hicklin. I thank the community of Saltcoats, especially James Jowsey, Verne and Joann Neil, Dee Dee and Hudson Walker, Dean and Irene Maddaford, Steve and Joanne Conklin, Jack Dawes, Merin Toth, and all the other landowners who gave me assistance and support throughout the field seasons. I thank the staff of Ducks Unlimited Canada, Yorkton office, Ron Anderson, Karen Nadeen, Wendy Lyon-Eskowich, Dwight Knapik, Betsy Didrickson, Scott Swengel, and Tim Bischof for their support.

Documents Cited

Lyon, W. J., D. Hjertaas, and **B. W. Johns**. 1995. Development of screening criteria and identification of potential reintroduction sites for the Whooping Crane in prairie Canada. Unpublished report. Canadian Plains Research Centre.

Nesbitt, S. A. 1988. An evaluation of the Florida Sandhill Crane population of peninsular Florida and its potential to support a population of non-migratory Whooping Cranes. Unpublished report. Florida Game and Fresh Water Fish Commission.

Schmidt, A. 1973. An ecological survey of the Yorkton wetland complex. Unpublished report. Department of Natural Resources, Wildlife Research.

Literatre Cited

Archibald, G. W. 1976. Crane taxonomy as revealed by the unison call. Pages 225-251 *in* Proceedings of the [1975] International Crane Workshop. *Edited by* J. C. Lewis. Oklahoma State University, Stillwater, Oklahoma.

Armbruster, M. J. 1987. Habitat suitability index models: Greater Sandhill Crane. U.S. Fish and Wildlife Service Biological Report 82.

Bennett, A. J. 1978. Auditory censusing of Greater Sandhill Cranes. Auk 95: 411-413.

Bird, R. D. 1961. Ecology of the aspen parkland of western Canada in relation to land use. Canadian Department of Agriculture Report Number 1066.

Bishop, M. A. 1988. Factors affecting productivity and habitat use of Florida Sandhill Cranes: an evaluation of three areas in central Florida for a non-migratory population of Whooping Cranes. Ph.D. dissertation, University of Florida, Gainesville, Florida.

Daubenmire, R. F. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33: 43-65.

DiMatteo, J. J. 1992. Status, production and migration of Greater Sandhill Cranes on Agassiz National Wildlife Refuge, Minnesota. Pages 13-20 *in* Proceedings of the 1988 North American Crane Workshop. *Edited by* D. A. Wood. Florida Game and Fresh Water Fish Commission Nongame Wildlife Program Technical Report Number 12, Tallahassee, Florida.

Drewien, R. C. 1973. Ecology of Rocky Mountain Greater Sandhill Cranes. Ph.D. dissertation, University of Idaho, Moscow, Idaho.

Drewien, R. C., W. M. Brown, and **W. L. Kendall.** 1995. Recruitment in Rocky Mountain Greater Sandhill Cranes and comparison with other crane populations. Journal of Wildlife Management 59: 339-356.

Duan, W., T. A. Bookhout, and **R. P. Urbanek.** 1997. Home range and habitat use by isolation-reared Sandhill Cranes. Pages 72-78 *in* Proceedings of the Seventh North American Crane Workshop. *Edited by* R. P. Urbanek and D. W. Stahlecker. North American Crane Working Group.

Edwards, R. S., S. Brechtal, R. Bromley, D. Hjertaas, B. Johns, E. Kuyt, J. Lewis, N. Manners, R. Stardom, and **G. Tarry**. 1994. National recovery plan for the Whooping Crane. Recovery of Nationally Endangered Wildlife Report Number 6.

Eldridge, J. 1990. Ecology of northern prairie wetlands. Waterfowl Management Handbook Leaflet 13(3.5). U.S. Fish and Wildlife Service.

Fisher, I. L., and **S. R. Swengel.** 1991. A guide for aging Sandhill Crane eggs. Wildlife Society Bulletin 19: 494-497.

Genter, D. L. 1985. Northern Harrier kills Sandhill Crane. Wilson Bulletin 97: 108-109.

Houston, C. S. 1949. The birds of the Yorkton District, Saskatchewan. Canadian Field-Naturalist 63: 215-241.

Johnsgard, P. A. 1983. Cranes of the world. Croom Helm, London.

Johnson, J. M. 1976. Territory, nesting and habitat utilization of Greater Sandhill Cranes in Morrison County, Minnesota. M. A thesis. St. Cloud University, St. Cloud, Minnesota.

Lewis, J. C. 1979. Field identification of juvenile Sandhill Cranes. Journal of Wildlife Management 43: 211-214.

Littlefield, C. D., and **S. M. Lindstedt.** 1992. Survival of juvenile Greater Sandhill Cranes at Malheur National Wildlife Refuge, Oregon. Pages 21–31 *in* Proceedings of the 1988 North American Crane Workshop. *Edited by* D. Wood. Florida Game Fresh Water Fish Commission Nongame Wildlife Program Technical Report 12, Tallahassee, Florida.

McMillen, J. L. 1988. Productivity and movements of the Greater Sandhill Crane population at Seney National Wildlife Refuge: potential for an introduction of Whooping Cranes. Ph.D. dissertation, Ohio State University, Columbus, Ohio.

McMillen, J. L., S. A. Nesbitt, M. A. Bishop, A. J. Bennett, and **L. A. Bennett.** 1992. An evaluation of three areas for potential populations of Whooping Cranes. Pages 285-289 *in* Proceedings of the 1988 North American Crane Workshop. *Edited by* D. Wood. Florida Game Fresh Water Fish Commission Nongame Wildlife Program Technical Report 12, Tallahassee, Florida.

Meine, C., and **G. W. Archibald.** 1996. The cranes: status, survey and conservation action plan. IUCN, Gland, Switzerland.

Millar, J. B. 1976. Wetland classification in western Canada. Canadian Wildlife Service Report Series 37.

National Wetlands Working Group. 1988. Wetlands of the prairies of Canada. Canadian Wildlife Service Ecological Land Classification Series 24.

Nesbitt, S. A. 1992. First reproductive success and individual productivity in Sandhill Cranes. Journal of Wildlife Management 56: 573-577.

Provost, J. L., T. A. Provost, S. J. Maxson, and **R. D. Crawford.** 1992. Breeding biology of Greater Sandhill Cranes on the Roseau River Wildlife Management Area, Minnesota. Pages 69-74 *in* Proceedings of the Sixth North American Crane Workshop. *Edited by* D. W. Stahlecker. North American Crane Working Group.

Reed, C. A. 1903. North American bird eggs. Reprint 1965, Dover Publications, New York.

Robel, R. J., J. N. Briggs, A. D. Dayton, and **L. C. Hulbert.** 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23: 295-297.

Rowe, J. S. 1987. Status of the aspen parkland in the prairie provinces. Pages 27-33 *in* Proceedings of the Workshop on Endangered Species in the Prairie Provinces. Alberta Culture Historical Resources Division Occasional Paper 9.

Stern, M. A., G. J. Pampush, and **R. E. Carlo**. 1987. Nesting ecology and productivity of Greater Sandhill Cranes at Sycan Marsh, Oregon. Pages 249-256 *in* Proceedings of the 1985 Crane Workshop. *Edited by* J. C. Lewis. Platte River Whooping Crane Maintenance Trust, Grand Island, Nebraska.

Strong, W. L., and **K. R. Leggat.** 1981. Ecoregions of Alberta. Alberta Department of Energy and Natural Resources Technical Report T/4.

Tacha, T. C. 1988. Social organization of Sandhill Cranes from midcontinental North America. Wildlife Monographs 99: 1-37.

Tacha, T. C., P. Vohs, and **G. C. Iverson**. 1984. Migration routes of Sandhill Cranes from mid-continental North America. Journal of Wildlife Management 48: 1028-1033.

Tacha, T. C., S. A. Nesbitt, and **P. Vohs.** 1992. Sandhill Crane (*Grus canadensis*). The Birds of North America, Life Histories for the 21st Century, number 31. American Ornithologists' Union.

Turner, B. C., G. S. Hochbaum, F. D. Caswell, and **D. J. Nieman.** 1987. Agricultural impacts on wetland habitats on the Canadian prairies, 1981-1985. Pages 206-215 *in* Transactions of the 52nd North American Wildlife and Resources Conference. *Edited by* Wildlife Management Institute, Washington, D. C.

Walkinshaw, L. H. 1973. Cranes of the world. Winchester Press, New York, New York.

Received 9 November 2001
Accepted 13 August 2003

Physical Condition of an Animal, Using as an Example the Common Eider, *Somateria mollissima*

ARNAUD J. CABANAC

Département de Biologie, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, Québec G5L 3A1 Canada
Present address : Parc Aquarium du Québec, 1675 avenue des Hôtels, Sainte-Foy, Québec G1W 4S3 Canada

Cabanac, Arnaud J. 2003. Physical condition of an animal, using as an example the Common Eider, *Somateria mollissima*. Canadian Field-Naturalist 117(2): 230-235.

An index of the physical condition of an animal should describe its endogenous available energy. The welfare of the animal depends on its ability to spend its stored energy (lipid and protein) in order to survive the environmental and behavioural challenge at the particular time of its capture. I propose a new index to predict the survival chance of the subject. The new index of physical condition takes into account the available endogenous energy reserves and the known needs of the species at that particular time of year. I further illustrate this new method of estimating the physical condition by running a trial with Common Eiders, *Somateria mollissima*.

Key Words: Behaviour, ecology, physiology, management, fitness.

An index of physical condition of an animal is usually obtained by integrating the energy reserve of the organism under consideration and its ability to spend this energy (Evans and Smith 1975; Ringelman and Szymczak 1985; Blem 1990). In the wild, fasting is known to happen routinely, either voluntarily, for example in birds as a reproductive strategy to protect the nest, or involuntarily because of food shortage (e.g., Mrosovsky and Sherry 1980; Drent and Daan 1980; Blem 1990; Wingfield et al. 1997). Knowing whether some individuals, or an entire population, are in good physical condition is therefore a difficult task but it is more than often a basic question for ecologists and ethologists.

Physiology

The energy reserve is usually evaluated through analysis of the subject's body composition. Originally, fat was considered as the animal's only energy reserve (e.g., Odum et al. 1964; Pond 1978; Griminger 1986), but recent literature on body composition in birds underlined that muscle tissues are also a labile energy store (e.g., Evans and Smith 1975; McLandress and Raveling 1981; Cherel et al. 1988; Lindström and Piersma 1993; Choinière and Gauthier 1995). Further, it is also known that the body can better tolerate lipid than protein depletion. The lipid reserves can go close to total depletion (e.g., Gorman and Milne 1971; Milne 1976; Korschgen 1977; Pond 1978; Groscolas 1986; Robin et al. 1988; Parker and Holm 1990; Boismenu et al. 1992) whereas more than 30-50% decrease of protein content leads mammals and birds to death (e.g., Montemurro and Stevenson 1960; Garrow et al. 1965; Gorman and Milne 1971; Peret and Jacquot 1972; Parker and Holm 1990; Boismenu et al. 1992). This implies that lipids have to be stored in the adipose tissue in order to delay protein breakdown and its lethal diminution to anticipate and counter food shortage. In seals, the proteins sustained only 4-8% of the metabolism during 52 d of fasting (Nordøy et al. 1990). The corresponding figures in geese and penguins, were 6% over 40 d (Le Maho et al. 1981), and 4% over 90 d of fasting (Robin et al. 1988). This is certainly the main reason for the high survival of these animals in extreme conditions. The knowledge of lowered but yet present protein breakdown was lacking in 1969 when obese humans underwent long-term fasting as treatment for obesity, and deaths occurred even though the patients still had huge fat stores at the time of their deaths (Barnard et al. 1969). This example casts light on the fact that both lipid and protein contents are important energy reserves that must both be taken under consideration to estimate the subject's welfare.

Several studies on fasting birds have shown that, in penguins (e.g., Le Maho et al. 1976; Cherel and Le Maho 1985; Robin et al. 1988) and in geese (e.g., Le Maho et al. 1981; Cherel et al. 1988; Boismenu et al. 1992), the loss in weight due to food shortage follows three different rates of decrease when graphically plotted against time. The above references are summarized in Table 1, which gives the time course of weight loss in three periods. Period I would last only a few days and the rate of weight loss in this first period is relatively high. It corresponds to the use of the glycogen stores and is associated with a drop in protein utilization. Period II is marked by the use of fat as the main metabolic fuel, with a slower decrease in body weight over time. This second period could last several weeks. Period III would last several days during which amino acids fulfill the energy requirements. This third and last period is marked by an increase in protein breakdown and a sharp increase in the subject's weight loss. The three periods of Table 1, which are proposed from bird data, apply as well to fasting mammals; e.g., humans

TABLE 1. Summary in three periods of time for weight loss during fasting.

Period	Duration	Physiology	Source of energy
I	1-2 days	fast weight loss (decreasing rate)	glycogen & protein
II	weeks	slow weight loss (stable rate)	fat
III	5-6 days	fast weight loss (increasing rate)	protein

(Cahill 1976) and seals (Nordøy et al. 1990). It appears clearly therefore that, to have a realistic estimate of the survival chance of an organism, one should distinguish fat from lean mass in body composition analysis (see also Blem 1990; Van der Meer and Piersma 1994). [The integrated response to fasting is only partially understood and is beyond the scope of the present work; for more on the subject of body weight stability see Mrosovsky 1990; Belkhou et al. 1990; Cabanac et al. 1999.]

Thus, by definition, the index of physical condition should indicate on the subject's ability to spend its energy (Ringelman and Szymczak 1985) or, as stated by Evans and Smith (1975), on its chance of survival at a particular time of year. This is so, because the score of an animal having low reserves of energy may not represent the same physical condition in spring as in fall. The variables chosen to represent energy demand are usually size-related measures, such as body masses, with or without association of some structural measurements (e.g., Odum et al. 1964; Child 1969; Evans and Smith 1975; Ringelman and Szymczak 1985; Johnson et al. 1985; Moser and Rusch 1988; also Blem 1990; Piersma and Davidson 1991; Chastel et al. 1995). However, little attention has been paid to the different amounts of energy loss that could be tolerated in the subject's various periods of life.

In the following I propose a physical condition index (PCI) that takes into account not only the available body reserves but also the time of year. The index is based on how much protein and lipid an organism could maximally lose in the particular periods of its life. This index describes and predicts the subject's welfare. I chose to test estimating the ability of the bird to survive from the size of its energy reserve, on the Common Eider because the biology of that large duck is well documented, but a similar exercise could equally well have used a mammal.

Natural History of the Common Eider

Unstable body weight

In Common Eiders, *Somateria mollissima*, females feed very little or not at all from laying to hatching (Gorman and Milne 1971; Cantin et al. 1974; Milne 1976; Korschgen 1977; Parker and Holm 1990). In such long-term spontaneous fasting, the metabolism of the bird is fueled solely by endogenous energy reserves. Consequently, such behaviour is reflected in massive weight loss by the ducks. During the 22-26 days of the incubation period, a female loses 22-42% of its weight (29.5%, Korschgen 1977; 35.2%, Kuresoo and Paakspuu 1983; 22.3%, Parker and Holm 1990; 35.6%, Gabrielsen et al. 1991; 41.6%, Bolduc and Guillemette 2003). Further, Parker and Holm (1990) reported that the breeding females also fasted for about 6-7 additional days before incubating and that such eiders would have used already about 34% of their stored energy at that time. Previous reports mentioned a 20-21% increase in body weight of females that will breed in the next summer (Milne 1976; Korschgen 1977; Parker and Holm 1990). This gain in weight was designated as "the storage of nutrients and energy necessary for egg production", as it corresponds to about the weight that will be lost by the females during the following laying period (Korschgen 1977; Parker and Holm 1990). Therefore, in total, a female eider would lose 44-54% of its weight during 28-33 d of the laying and incubating periods (Cantin et al. 1974; Milne 1976; Korschgen 1977; Parker and Holm 1990; Gabrielsen et al. 1991), 19% of which would be the clutch weight (Parker and Holm 1990). This impressive weight loss of a breeding female eider is similar to the 39-44% weight loss reported in geese after 34-40 d of fasting (Le Maho et al. 1981; Boismenu et al. 1992) and to the 52% and 68% of weight loss of Emperor Penguin, *Aptenodytes forsteri,* and King Penguin chicks after a four-month and a five-month fasting period (Robin et al. 1988; Cherel and Le Maho 1985).

Fasting may also happen involuntarily in the wild because of food shortage. In condition of extreme food shortage a fasting eider may totally deplete its metabolic reserves. Wårnes (1988) reported that some starving eiders lost 35-39% of their weight during the winter 1982. Also, Kervella and M. Guillemette (unpublished observation) measured a 21.3-24.8% weight loss in starving eiders (males and females) from the Gulf of St. Lawrence in winter 1999. These eiders were exposed accidentally to oil-polluted water along the coast of the Gulf of St Lawrence in March 1999 and were apparently unable to feed (see also Hartung 1967; Gorman and Milne 1971).

Interestingly, in these two examples of fasting eiders, the populations starving in winter lost about the same weight (21.3-24.8% and 35-39%) before dying as what the female is capable of losing during the incubation period (22-42%), and much less than these females if the laying period is taken into account (Parker and Holm 1990). It makes sense that a heavier female (because of its increased weight in anticipation of the

breeding period seen above), can lose more weight than a thinner one that did not accumulate such reserves. However, this suggests different types of body weight loss, thus allowing survival during the reproduction season.

Energy reserve

Several studies have shown that eiders, like other birds and mammals, use both fat and protein reserves as endogenous sources of energy (Milne 1976; Korschgen 1977; Parker and Holm 1990). Further, Milne (1976) measured the gross variation in body weight, protein, and lipid content during the natural fast of the breeding period. We can also discriminate in eiders, in Milne's (1976) figure 1, the above-defined Periods I, II, and III on fasting geese and penguins. Milne (1976: figure 1) indicated that from mid-April to mid-June, the protein content diminished only weakly, but the fat content decreased sharply, resulting in a drop of body weight. As seen above, these changes mimic the definition of Period II. A sharp decrease of the eiders' protein content starts between mid-June and early July and lasts until the end of incubation. This later period would correspond to Period III. Period I is reportedly difficult to identify and probably would occur in the first days of laying. Our interpretation of Milne's (1976) results certainly deserves additional work. However, the results of Gabrielsen et al. (1991) may be similarly viewed: they concluded that fat was the major fuel during incubating fasting eiders, which would tend to confirm my hypothesis of a similar physiology in the utilization of energy reserve in fasting eiders, as that well-known for geese and penguins. Also, Parker and Holm (1990) measured only a smaller rate of protein loss during the incubation period (1.9 g/day) than that measured during the few days of the laying period (16.8 g/day).

Index of physical condition of the eider

It follows from the above considerations that an index of body condition should integrate the bird's body weight, which can fluctuate over time, but also its lipid and protein contents, to provide an accurate estimate of the available energy reserves at the moment of its capture. Further, we saw above that the interpretation of protein and fat reserves, in terms of the bird's welfare, would not be the same if the duck were sampled in winter, vs. during the breeding period. Thus, for the following, I collected available data from the literature on body weight and lipid and protein contents in wintering and breeding eiders, to estimate the energy reserve for a typical eider sampled in these periods. It must be hypothesized therefore that profound physiological changes take place during the year, allowing longer fasting without deleterious results during the reproductive season. This leads me to propose an index with different parameters for these two periods in the bird's year. Two reports were available:

Cabanac and Guillemette (unpublished observation) correlated lipid and protein contents with body mass on 127 wintering eiders, and obtained the following equations:

Lipid = 0.165 (body weight) -168.7 (Equation 1)

Protein = 0.142 (body weight) +49.4 (Equation 2)

There were no differences between males and females.

Korschgen (1977) correlated the same variables for females during the incubating period and reported the following equations:

Lipid = 0.420 (body weight) -444.4 (Equation 3)

Protein = 0.160 (body weight) +48.0 (Equation 4)

Exhaustion threshold

Starving or near-starving-to-death eiders (males and females) were studied by Gorman and Milne (1971); their lipid content was lowered down by 95% over a winter. In the breeding period, several studies reported similar results in females, which became totally depleted of fat by hatching; yet these females recovered thereafter (Milne 1976; Korschgen 1977; Parker and Holm 1990). Thus, if we remove fat from equations 1 & 3 (lipid equal to zero) it follows that body weight of these fat-depleted eiders would theoretically correspond to 1022 g in winter (derived from Equation 1: body weight = 168.7/0.165), and to 1058 g during the incubation period (derived from Equation 3: body weight = 444.4/0.420). As seen above in the physiology of fasting, eiders of lightest body weights in both periods would get their energy from protein breakdown, and would be in Period III of the fasting metabolism (short period of increased catabolism of proteins for neoglucogenesis). However, a female eider is known to raise its protein content before laying (Milne 1976; Parker and Holm 1990), and this slight boost in protein content may explain some of the small discrepancy of body weight of fat-depleted eiders in winter and in the breeding period.

Spontaneously fasting females of the breeding period were shown to endure protein depletion up to 37% (Parker and Holm 1990), and even 50% (Gorman and Milne 1971). Moreover, Korschgen (1977) reported some eiders at the beginning of the laying period to weigh 2530 g, which when incorporated into Equation 4 suggested 453 g was protein (Protein = 0.160 (2530) +48.0). Equation 3 predicts that in the breeding period a fat-depleted eider would weigh 1058 g, which when incorporated into Equation 4 suggested 217 g was protein (Protein = 0.160 (1058)+48.0). This suggests that the protein content in a fat-depleted eider would correspond to a 52% reduction. Considering that an eider depleted of lipid would be in its critical Period III, it is likely that such protein depletion would be close to the maximal endurance of protein breakdown. Thus, at the end of incubation, Gorman and Milne's (1971) results with 50% of protein depletion would indicate that some females might approach their physiological limit at the time of hatching, as is known to occur.

On the other hand, during the winter, starving, or near-to-death starving, eiders (males and females) were reported to have their protein content diminished only by about 23% at the moment of their death (Gorman and Milne 1971). The discrepancy of protein utilization of wintering eiders and breeding eiders suggests that a female in the breeding period could endure more protein breakdown than during the winter. However, the wintering eiders of Gorman and Milne's (1971) study were oil-contaminated, and a possibly lethal contamination by petroleum may have acted on the birds' endurance of protein depletion (possibly lowering it). In a study on the body composition of some 131 wintering eiders of the Gulf of St. Lawrence, we obtained (Cabanac and Guillemette, unpublished observations) an average body weight of 1815 g for both females and males, of which 307 g protein (Equation 2). With Equation 1 I can predict that in the winter period a fat-depleted eider would weigh 1022 g, of which 195 g is protein (Equation 2). This suggests that the protein content in a fat-depleted eider would correspond to about a 37% reduction. Again, considering that an eider depleted of lipid would be in its critical Period III, I believe that such protein depletion would be close to the maximal endurance of protein breakdown of wintering eiders.

Physical Condition Index (PCI)

The Index of Physical Condition (PCI) corresponds to the endogenous reserves content in lipid and protein correlated to the body weight at that time (winter and breeding period), minus the maximal rate of utilization of protein and lipid. The maximal utilization of endogenous energy was shown to be 95% of the lipid, both in winter and during the breeding period; the maximal utilization of protein in those periods was 37% and 52%, respectively, corresponding to fat-depleted eiders. From these data I may now propose the following indexes describing physical condition during the two different periods (where F and P are fat and protein mass expressed in g):

Wintering $PCI = 0.05*F + 0.63*P$ (Equation 5)
Breeding $PCI = 0.05*F + 0.48*P$ (Equation 6)

The equation is the same in both periods, but the parameters change for wintering and breeding eiders. Because these equations use the minimal energy contents, the index describes the lowest physical condition that an average eider could sustain in each period. If an individual scored below those critical levels, its survival should be compromised.

Examples

Data from the literature on body composition of several Common Eiders, permits a check on the validity of this new PCI. The results are indicated in Table 2 and the mean results are illustrated in Figure 1:

Common Eiders in the pre-laying period are, as we have seen above, supposedly in good physical condition, and their mean (±s.d.) PCI was:

PCI = 245.1±5.45

The PCI of eiders at the end of the voluntary fasting period, a time of poor physiological conditions, was:

PCI = 125.4±10.00

Thus, these results seem to support the validity of the new PCI. Moreover, an eider in the laying period should have already burnt some valuable amount of energy (as seen above) but would still have to run the entire incubating period. Accordingly, its intermediary value for PCI (PCI = 187.0±17.41) was similar to that of the eiders in the pre-laying and the hatching periods as shown in Figure 1.

The physical condition index can be applied to groups of eiders of unknown welfare to find out their probability of survival. Of course, the calculation implies the sacrifice of some individuals, but the results will inform the researcher on the state of the population. The index is easy to obtain; it needs only the body weight (and carcass analysis if the subject is measured out of the periods of validity of our PCI) of the individual to be evaluated, and the period of the year corresponding to its capture. Similar reasoning could be applied to individuals at the winter period. PCI in winter corresponded to 200.0 (Table 2). For example in winter 1999, a small ecological catastrophe (oil slick) happened at Havre-Saint-Pierre: Some eiders were unable to feed and also suffered hypothermia due to damaged plumage; over 1000 eiders died (Kervella and

TABLE 2. Physical condition index (PCI) of some Common Eiders, as obtained from the body weight of the ducks and from Equations 3, 4, and 6 for Pre-laying, Pre-incubating, and Hatching periods, and from Equations 1, 2, and 5 for Wintering eiders.

PRE-LAYING PCI (bodyweight, g)	PRE-INCUBATING PCI (body weight, g)	HATCHING PCI (body weight, g)	WINTERING PCI (body weight, g)	SOURCE
245.3 (2500)		113.3 (1150)		Milne 1976
	179.9 (1830)	121.2 (1232)		Korschgen 1977
250.5 (2553)	174.2 (1773)	133.8 (1368)		Parker and Holm 1990
239.6 (2442)	206.8 (2106)	133.5 (1357)		Gabrielsen et al. 1991
			200.0 (1817)	Cabanac and Guillemette, *unpublished*
245.1±5.45	187.0±17.41	125.4±10.00	200.0	Mean PCI (± s.d.)

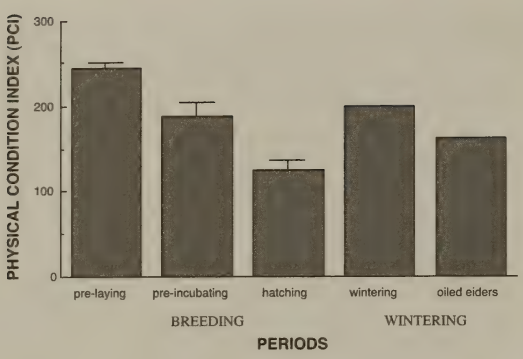


FIGURE 1. Physical condition index (PCI) for breeding (pre-laying, laying, and incubating) and wintering Common Eiders. PCI withdraw the energy required by the subject at that particular time of year from the endogenous reserves (lipid and protein). In breeding eiders, PCI is illustrated for the pre-laying, the laying, and the incubating periods; in winter, healthy ducks and oiled eiders are represented.

Guillemette, unpublished observation): at autopsy the males weighed 1469 g and the females 1397 g (mean 1433 g), which with Equations 1, 2, and 5, corresponds to PCI = 162.7. Interestingly this figure is much lower than the PCI computed for the wintering eiders (Table 2, Figure 1); this would indicate that these eiders were in bad physical condition.

Wildlife Management

I have shown that a physical condition index is easy to obtain. An accurate estimation of the energy reserve (lipid and protein) of the organism under consideration is necessary, together with an integration of its ability to survive. The PCI provides an estimate of the subject's chance of survival at a particular time of the year obtained by withdrawing the energy required by the animal at that particular time of year from the endogenous reserves. I have shown that such a method works at least for Common Eiders, but I believe that a similar protocol could be applied to other wildlife and would facilitate their management.

Acknowledgment

The research was supported by a CRSNG-NSERC Government of Canada postdoctoral fellowship.

Literature Cited

Barnard, D. L., J. Ford, E. S. Garnett, R. J. Mardell, and **A. E. Whyman.** 1969. Changes in body composition produced by prolonged total starvation and refeeding. Metabolism 18: 564-569.

Belkhou, R., J.-P. Robin, Y. Cherel, and **Y. Le Maho.** 1990. Utilization of lipid versus protein reserves during long-term fasting in mammals and birds. Pages 231-241 *in* Animal nutrition and transport process. *Edited by* Mellinger, Basel, and Karger. Comparative Physiology 5.

Blem, C. 1990. Avian energy storage. Current Ornithology 7: 59-113.

Boismenu, C., G. Gauthier, and **J. Larochelle.** 1992. Physiology of prolonged fasting in Greater Snow Geese (*Chen caerulescens atlantica*). Auk 109: 511-521.

Bolduc, F., and **M. Guillemette.** 2003. Incubation constancy and mass loss in the Common Eider (*Somateria mollissima*). Ibis 145: 329-332.

Cabanac, M., C. Michel, and **C. Gosselin.** 1999. Corticotropin Releasing Hormone and body weight regulation: the behavioral approach. Nutritional Neuroscience 2: 385-401.

Cahill, G. F. 1976. Starvation in man. Journal of Clinical Endocrinology and Metabolism 5: 397-415.

Cantin, M., J. Bédard, and **H. Milne.** 1974. The food and feeding of common eiders in the St. Lawrence estuary in summer. Canadian Journal of Zoology 52: 319-334.

Chastel, O., H. Weimerskirch, and **P. Jouventin.** 1995. Body condition and seabird reproductive performance: a study of three petrel species. Ecology 76: 2240-2246.

Cherel, Y., and **Y. Le Maho.** 1985. Five months of fasting in king penguin chicks: body mass loss and fuel metabolism. American Journal of Physiology 249: R387-R392.

Cherel, Y., J.-P. Robin, and **Y. Le Maho.** 1988. Physiology and biochemistry of long-term fasting in birds. Canadian Journal of Zoology 66: 159-166.

Child, G. I. 1969. A study of nonfat weights in migrating Swainson's Thrushes (*Hylocichla ustulata*). Auk 86: 327-338.

Choinière, L., and **G. Gauthier.** 1995. Energetics of reproduction in female and male greater snow geese. Oecologia 103: 379-389.

Drent, R. H., and **S. Daan.** 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.

Evans, P. R., and **P. C. Smith.** 1975. Studies on shorebirds at Lindisfare, Northumberland. II. Fat and pectoral muscle as indicators of body condition in the Bar-tailed Godwit. Wildfowl 26: 64-76.

Gabrielsen, G. W., F. Mehlum, H. E. Karlsen, Ø. Andersen, and **H. Parker.** 1991. Energy cost during incubation and thermoregulation in the female Common Eider *Somateria mollissima*. Norsk Polarinstitutt Skrifter 195: 51-62.

Garrow, J. S., K. Fletcher, and **D. Halliday.** 1965. Body composition in severe infantile malnutrition. Journal of Clinical Investigation 44: 417-425.

Gorman, M., and **H. Milne.** 1971. Seasonal changes in the adrenal steroid tissue of the Common Eider *Somateria mollissima* and its relation to organic metabolism in normal and oil-polluted birds. Ibis 113: 218-228.

Griminger, P. 1986. Lipid metabolism. Pages 345-358 *in* Avian physiology. *Edited by* P. D. Sturkie. Springler-Verlag, New York.

Groscolas, R. 1986. Changes in body mass, body temperature and plasma fuel levels during the natural breeding fast in male and female emperor penguins *Aptenodytes forsteri*. Journal of Comparative Physiolology–B 156: 521-527.

Hartung, R. 1967. Energy metabolism in oil covered ducks. Journal of Wildlife Management 31: 798-804.

Johnson, D. H., G. L. Krapu, K. L. Reinecke, and **D. G. Jorde.** 1985. An evaluation of condition indices for birds. Journal of Wildlife Management 49: 569-575.

Korschgen, C. E. 1977. Breeding stress of female eiders in Maine. Journal Wildlife Management 41: 360-373.

Kuresoo, A., and **V. Paakspuu.** 1983. Physiological starvation and its adaptative role in the breeding-cycle of diving

ducks. Communication of the Baltic Commission for the Study of Bird Migration 15: 83-92.

Le Maho, Y., P. Delclitte, and **J. Chatonnet.** 1976. Thermoregulation in fasting emperor penguins under natural conditions. American Journal of Physiology 231: 913-922.

Le Maho, Y., H. V. Van Kha, H. Koubi, G. Dewasmes, J. Girard, P. Ferré, and **M. Cagnard.** 1981. Body composition, energy expenditure, and plasma metabolites in long-term fasting geese. American Journal of Physiology 241 (Endocrinology and Metabolism 5): E342-E354.

Lindström, Å., and **T. Piersma.** 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. Ibis 135: 70-78.

McLandress, M. R., and **D. G. Raveling.** 1981. Changes in diet and body composition of Canada Geese before spring migration. Auk 98: 65-79.

Milne, H. 1976. Body weights and carcass composition of the Common Eider. Wildfowl 27: 115-122.

Montemurro, D. G., and **J. A. F. Stevenson.** 1960. Survival and body composition of normal and hypothalmic obese rats in acute starvation. American Journal of Physiology 198: 757-761.

Moser, T. J., and **D. H. Rusch.** 1988. Indices of structural size and condition of Canada Geese. Journal Wildlife Management 54: 202-208.

Mrosovsky, N. 1990. Rheostasis, The physiology of change. Oxford: Oxford University Press. 183 pages.

Mrosovsky, N., and **D. F. Sherry.** 1980. Animal anorexias. Science 207: 837-842.

Nordøy, E. S., O. C. Ingebretsen, and **A. S. Blix.** 1990. Depressed metabolism and low protein catabolism in fasting grey seal pups. Acta Physiologica Scandinavica 139: 361-369.

Odum, E. P., D. T. Rogers, and **D. L. Hicks.** 1964. Homeostasis of the nonfat components of migrating birds. Science 143: 1037-1039.

Parker, H., and **H. Holm.** 1990. Patterns of nutrient and energy expenditure in female Common Eiders nesting in Svalbard. Auk 107: 660-668.

Peret, J., and **R. Jacquot.** 1972. Nitrogen excretion on complete fasting and on a nitrogen-free diet-endogenous nitrogen. Pages 73-118 *in* International encyclopedia of food and nutrition. Protein and amino acid functions. Volume II. *Edited by* E. J. Bigwood, Pergamon Press, Oxford.

Piersma, T., and **N. C. Davidson.** 1991. Commentaries: Confusions of mass and size. Auk 108: 441-444.

Pond, C. M. 1978. Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. Annual Reviews Ecological System. 9: 519-570.

Ringelman, J. K., and **M. R. Szymczak.** 1985. A Physiological condition index for wintering mallards. Journal of Wildlife Management 49: 564-568.

Robin, J-P., M. Frain, C. Sardet, R. Groscolas, and **Y. Le Maho.** 1988. Protein and lipid utilization during long-term fasting in emperor penguins. American Journal of Physiology 254: R61-R68.

Van der Meer, J., and **T. Piersma.** 1994. Physiologically inspired regression models for estimating and predicting nutrient stores and their composition in birds. Physiological Zoology 67: 305-329.

Wårnes, E. 1988. Massedød av aerfugl på Sørlandet vinteren 1981/82. Vår Fuglefauna 11: 71-74.

Wingfield, J. C., K. Hunt, C. Breuner, K. Dunlap, G. S. Fowler, L. Freed, and **J. Lepson.** 1997. Environmental stress, field endocrinology, and conservation biology. Pages 95-131 *in* Behavioral approaches to conservation in the wild. *Edited by* Clemmons and Buchholz Cambridge University Press, Cambridge, U.K.

Received 3 December 2001
Accepted 15 September 2003

Phenotypic Variation in Skull Size and Shape Between Newfoundland and Mainland Populations of North American Black Bears, *Ursus americanus*

JOHN A. VIRGL[1], SHANE P. MAHONEY[2], and KIM MAWHINNEY[3]

[1]Ecological Development and Statistical Analysis, 222 Haight Place, Saskatoon, Saskatchewan S7H 4W2 Canada
[2]Science Division, Wildlife and Protected Areas, P. O. Box 8700, Department of Tourism, Culture, and Recreation, St. John's, Newfoundland A1B 4J6 Canada
[3]Canadian Wildlife Service, Environment Canada, 6 Bruce Street, Mount Pearl, Newfoundland A1N 4T3 Canada

Virgl, John A., Shane P. Mahoney, and Kim Mawhinney. 2003. Phenotypic variation in skull size and shape between Newfoundland and mainland populations of North American Black Bears, *Ursus americanus*. Canadian Field-Naturalist 117(2): 236-244.

It is well recognized that differences in environmental selection pressures among populations can generate phenotypic divergence in a suite of morphological characteristics and associated life history traits. Previous analysis of mitochondrial DNA and body size have suggested that Black Bears (*Ursus americanus*) inhabiting the island of Newfoundland represent a different subspecies or ecotype from mainland populations. Assuming that body size covaries positively with skull size, we predicted that skull size would be greater for bears on the island than the mainland, and the distribution of size-related shape components in multivariate space should show a distinct separation between Newfoundland and mainland populations. Measurements of 1080 specimens from Newfoundland, Alberta, New York, and Quebec did not provide unequivocal support for our prediction that skull size in Newfoundland bears would be larger than bears from the mainland populations. After removing ontogenetic effects of skull size, between-population variation in skull shape was greater in females than males, and the analysis significantly separated Newfoundland bears from mainland populations. Explanations for this pattern are numerous, but currently remain hypothetical. Limited covariation between skull size and body size suggests that genetic traits regulating the size of Black Bear skulls are more heritable (i.e., less influenced by environmental selection pressures) than characteristics affecting body size. We hypothesize that if gape size does not limit prey size in solitary terrestrial carnivores, large degrees of among-population variation in body size should be coupled with little covariation in skull size. In general, sexual dimorphism in skull size and shape was marginal for the phenotypic characters measured in our study. We believe that sexual dimorphism in skull size in Black Bears is primarily driven by intrasexual selection in males for increased gape size display, while similarity in skull shape between sexes is associated with the constraints of a temporally-selective, but similar diet.

Key Words: Black Bear, *Ursus americanus*, heritability, ontogeny, multivariate analysis, Newfoundland.

Several studies have used multivariate and univariate techniques on skull and jaw characteristics of carnivores to separate taxonomic groups or generate testable hypotheses about the processes driving morphological variation within species and between sexes (Rausch 1963; Ralls and Harvey 1985; Wiig 1989; Gittleman and Valkenburgh 1997; Chestin and Mikeshina 1998). Determining the relative importance of environmental selection and genetic factors (i.e., degree of heritability) on phenotypic covariance/variance among populations is fundamental for understanding the evolutionary divergence of populations into distinct species or subspecies (Felsenstein 1988; Armbruster and Schwaegerle 1996). However, while some phenotypic traits may respond quickly to local environmental conditions and result in measurable differences among geographically distinct populations, other characteristics may be inherently less flexible and exhibit little or no difference among populations. For example, pleiotropy, gene linkage, and/or phylogeny can constrain natural selection and limit the evolutionary divergence of one or more phenotypic characteristics (Harvey and Mace 1982; Lande 1982; Arnold 1992). Furthermore, as demonstrated by Roff (2000) in a genetic analysis of body size, growth rate, fecundity and development, it is not always possible to predict the direction of covariation among phenotypic traits.

Black Bears (*Ursus americanus*) on the island of Newfoundland were originally described as a new subspecies (*U. a. hamiltoni*) based on several cranial characteristics of 19 skulls from eastern Canada (Cameron 1956). Despite this limited sample, recent mitochondrial DNA analysis has provided partial support for the subspecies status of this population (Paetkau and Strobeck 1996). These authors suggested that the limited genetic divergence between Newfoundland and mainland populations occurred after the Wisconsin ice age through rapid genetic drift in a small isolated founder population (Paetkau and Strobeck 1996). Furthermore, a recent analysis of body size in Black Bears between Newfoundland and five mainland populations indicated that Newfoundland bears were significantly larger than individuals on the mainland (Mahoney et al. 2001). Larger size in Newfoundland

bears was theoretically attributed to a number of environmental selection pressures; the principal factor being the ability of an individual to exploit seasonally abundant and spatially dispersed dietary protein (Mahoney et al. 2001).

If historic/current differences in environmental selection pressures between island and mainland Black Bear populations exert similar effects on body size and skull size, then phenotypic variation in skull size between island and mainland populations should positively covary with patterns in body size. We examined this hypothesis through a multivariate analysis of four skull measurements from 1080 Black Bears collected from Newfoundland and three mainland populations. Specifically, we predicted that skull size would be greater for bears on the island than the mainland, and the distribution of size-related shape components in multivariate space should show a distinct separation between Newfoundland and mainland populations. We also report on the degree of sexual dimorphism among the four populations.

Materials and Methods

Skull measurements and geographic populations

Skulls were collected from four geographically distinct populations in North America: Alberta, Quebec, Newfoundland, and New York. Morphometric, sex, and age data were obtained from bears killed by hunters during the spring or autumn. A standard protocol, describing the linear measurements, units and precision, was used to ensure that the linear attributes for each measurement were identical (see below). Age of individuals, except young of the year, was determined using standard techniques for counting cementum annuli (Willey 1974). We accept that part of the phenotypic variation in skull size and shape may be associated with differences in size-dependent human hunting mortality, but assume that this selection mechanism is cursory in explaining the patterns observed here.

Four measurements were recorded to the nearest 1 mm. Condylobasal length (CBL) was measured as the distance, along the midline, from a line connecting the most posterior margins of the alveoli of the upper incisors to a line connecting the most posterior margins of the condyles. Zygomatic breadth (ZB) was recorded as the greatest distance across the zygomatic arches. Mastoid breadth (MB) was measured as the greatest width of the skull across the mastoid bones or processes. Mandibular length (ML) was recorded as the greatest length of one ramus of the lower jaw (not including any part of a tooth).

Statistical analysis

Data were pooled by sex and population to provide eight comparable groups, and all measurements were log-transformed prior to analysis (Wiig 1989; Lynch et al. 1997). These groups were then used to perform three separate analyses. The first two analyses examined among-population variation for females and males, independently. The third analysis used all eight groups in a single canonical variate analysis to calculate morphological (Mahalanobis, D^2) distance between sexes, which provides an index of sexual dimorphism (Wiig and Andersen 1986; Lynch et al. 1997).

When several groups (i.e., sexes and populations) are involved in a multivariate analysis, single group principal component analysis (PCA) is not suitable for separating the between-group structure expected among populations (Thorpe 1988; Wiig 1989). Therefore, we used the pooled within-group covariance matrix to conduct PCA (termed multiple group principal component analysis (MGPCA)) on skull measurements for female and male Black Bears from geographic populations. As with single group PCA, positive eigenvectors (correlation coefficients) for the morphometric measures indicate that the first principal component (PC1) in MGPCA is associated with size variation that can be explained by allometric or ontogenetic scaling (i.e., size-age relationship), and is uncorrelated with shape variation (Lynch et al. 1997). The remaining principal components (PCs) largely represent variation in skull shape. For each sex-specific PC, a one-way analysis of variance was conducted to examine the degree of between-population variation in skull size and shape components. The PCs were then entered into a canonical variate analysis (CVA) to test for significant multivariate differences among populations, while correcting for sample size. CVA was performed once using all PCs ("size-in" analysis) and a second time excluding PC1 ("size-out" analysis; Lynch and Hayden 1995; Lynch et al. 1997). Comparison of these two analyses provides a means of determining the contribution of size and size-related shape structure to the variation among populations (Lynch et al. 1997). Interpretation of the significance of shape components was based on asymptotic statistical procedures (Lynch et al. 1996). Reallocation rates were statistically compared to the expected 25% rate (100% / 4 groups) using Cohens Kappa (K) and associated 95% CI.

All statistical analyses were performed with the SAS statistical package for microcomputers (Version 6.07). SAS / IML programs for the MGPCA and Cohens Kappa were written and performed by John M. Lynch (Arizona State University).

Results

Geographic variation in skull size and shape

A total of 1080 Black Bear skulls ranging from cub of the year to 25 years of age were used in the analyses (Table 1). Non-parametric one-way ANOVA (Kruskal-Wallis test) indicated that there was significant variation in age composition among the sampled populations for female ($\chi^2 = 7.84$, $df = 3$, $P = 0.05$) and male ($\chi^2 = 16.14$, $df = 3$, $P < 0.01$) bear skulls. Much of this variation appears to be associated with the maximum age of skulls collected from the populations (Table 1). However, the median age of skulls

TABLE 1. Age composition (years) of skull samples for female and male Black Bears collected from geographic populations in North America. COY = cub of the year.

Population	Females			Males		
	N	Mean (min, max)	Median (95 Percentile)	N	Mean (min, max)	Median (95 Percentile)
Alberta	13	3.9 (COY, 13)	2 (13)	48	4.7 (COY, 16)	3 (13)
Newfoundland	154	5.2 (COY, 23)	4 (14)	265	5.4 (COY, 22)	4 (14)
New York	184	5.7 (1, 21)	4 (15)	263	4.3 (COY, 25)	3 (13)
Quebec	74	5.1 (1, 17)	4 (13)	79	3.9 (1, 20)	3 (10)

(2 – 4 years) and the 95 percentile (10 – 15 years) across populations indicates that there is a good representation of skulls that are approaching or have reached asymptotic size within all groups, except females from Alberta (four skulls were greater than four years of age).

Examination of the variation in three individual skull measurements among populations suggests that, on average, females from Newfoundland and New York have larger skulls than females from Alberta and Quebec (Table 2). Although Newfoundland females had slightly longer (CBL) and wider (MB and ZB) skulls than New York females, the difference was marginal compared to the other populations. In contrast, within males, bears from Alberta had the longest skulls (CBL), but skull breadth was similar among bears from Alberta, Newfoundland and New York, and smallest for individuals from Quebec (Table 2). For both sexes, patterns in jaw length (ML) showed little correlation with measurements of skull length and breadth.

Multiple group principal component analysis indicated that PC1 explained over 80% of the variation in female and male skull measurements within populations (%WGV), while PC2 and PC3 essentially accounted for all of the remaining variation (Table 3). PC1 was positively correlated with all four skull characteristics which constitutes significant ontogenetic or allometric size variation (Wiig 1992; Lynch et al. 1997). PC1 also explained a significant amount of between-population variation (%BGV) in female and male bears (Table 3), but did not separate Newfoundland from mainland populations (Figure 1). Similar to the data for individual skull measurements, PC1 indicated that females from Quebec have smaller skulls than females from Newfoundland and New York, while males from Quebec have smaller skulls than males from Newfoundland, New York and Alberta. These patterns of univariate and multivariate skull measurements do not support our prediction that Newfoundland Black Bears would have larger skulls than bears from mainland populations.

PC2 and PC3 were positively and negatively correlated with skull measurements which reflect variation in skull shape (Table 3). For females, all four skull measurements were significantly ($P < 0.05$) associated with PC2 and PC3, but within males, mastoid breadth was not significantly correlated with PC2. Within females, all three principal components resulted in a significant separation of the populations, but PC2 and PC3 explained more between-population variation than PC1. In contrast, the between-population variation accounted for by the three components was similar within males, and significant (Table 3). Overall, the results from the MGPCA indicate that PC1 is strongly associated with age-related changes in female and male skull size among Black Bear populations. Thus, the reader must be aware that PC1 not only contains growth-related changes in skull size, but also contains some variation in age composition among populations

TABLE 2. Mean ± 1 SE condylobasal length (CBL), mastoid breadth (MB), zygomatic breadth (ZB), and mandibular length (ML) for female (F) and male (M) North American Black Bears among populations. All variables were measured to the nearest 1 mm. ( ) = number of individuals. AB = Alberta, NFD = Newfoundland, NY = New York, QB = Quebec.

Population	CBL		MB		ZB		ML	
	F	M	F	M	F	M	F	M
AB	213.4 ± 12.4 (13)	288.8 ± 5.2 (48)	98.0 ± 6.0 (13)	120.7 ± 3.0 (48)	128.7 ± 8.1 (13)	157.0 ± 4.0 (48)	<60.0 ± 14.7 (13)	184.6 ± 1.1 48)
NFD	239.6 ± 1.6 (154)	257.2 ± 1.7 (265)	109.6 ± 1.0 (154)	119.8 ± 1.1 (265)	147.9 ± 1.7 (154)	160.0 ± 1.6 (265)	164.1 ± 1.2 (154)	176.9 ± 1.2 (265)
NY	233.3 ± 1.2 (184)	254.3 ± 1.5 (263)	106.9 ± 0.9 (184)	117.3 ± 1.0 (263)	142.8 ± 1.3 (184)	155.8 ± 1.5 (263)	171.0 ± 1.1 (184)	184.6 ± 1.1 (263)
QB	226.0 ± 2.7 (74)	234.4 ± 3.5 (79)	101.5 ± 1.4 (74)	103.8 ± 1.9 (79)	128.2 ± 3.6 (74)	135.3 ± 4.0 (79)	171.9 ± 3.1 (74)	172.7 ± 3.6 (79)

TABLE 3. Principal component coefficients for skull measurements within female and male Black Bears from four North American populations. Component coefficients are provided for those variables which have an asymptotic standard error to coefficient ratio greater than 3.0. All other coefficients were deemed to be not significant (NS). %WGV is the within-group variation explained by each component. %BGV is the between-group variation explained by each component. Results from ANOVAs (*F, P*) for examination of between-group differences for each component are also provided. Abbreviations for skull measurements are provided in Table 2.

	Females			Males		
	PC1	PC2	PC3	PC1	PC2	PC3
CBL	0.38	0.23	0.28	0.40	0.22	-0.14
MB	0.50	0.17	0.69	0.54	NS	-0.75
ZB	0.63	-0.73	-0.27	0.62	-0.66	0.42
ML	0.46	0.62	-0.61	0.41	0.72	0.49
%WGV	80.1	15.1	3.9	87.7	8.2	3.1
%BGV	6.8	12.9	14.4	7.3	8.4	5.2
F	10.29	20.87	23.69	17.21	19.82	12.00
P	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

(Table 1). PC2 and PC3 reflect between-population differences in size-related skull shape, but the relative amount of variation explained by these two components was greater within females than males.

Subsequent analysis of the canonical variates for "size-in" and "size-out" skull structure within females resulted in significant separation between most populations (Wilks' $\lambda > 0.64$, $P < 0.001$). After removing ontogenetic effects, Mahalanobis distances (corrected for sample size) between canonical variate scores indicated that female skull structure was different between all populations, except Alberta and New York (Figure 2). This result was confirmed by reallocation rates. For example, re-substitution of individual skulls to different populations was significantly ($P < 0.01$) greater than expected by chance for all populations ($K = 0.46 \pm 0.07$), except for Alberta and New York ($P = 0.05$, adjusted a for multiple comparisons = 0.008).

For male bears, there was also significant variation in "size-in" and "size-out" canonical variates between populations (Wilks' $\lambda > 0.77$, $P < 0.001$). Following removal of age-dependent size effects, re-substitution analysis indicated that only the Mahalanobis distance (corrected for sample size) between canonical variate scores for the Newfoundland and mainland populations was significant ($P < 0.01$). Thus, most of the individuals were being reallocated at a rate similar to that expected by chance ($K = 0.30 \pm 0.06$) which is exemplified by the large degree of overlap between populations from Alberta, Quebec and New York (Figure 2). Overall, these results support the prediction that size-related skull shape in female and male Newfoundland Black Bears would be significantly different than bears from the mainland populations.

Sexual Dimorphism

As expected for carnivores, skull length and skull breadth were greater in male bears than female bears (Table 2). The eight-group MGPCA indicated that all three principal components explained a significant amount of between-group variation ($P < 0.001$). The relative amount of between-group variance explained by PC1, PC2, PC3 was 14.2%, 10.9% and 8.5%, respectively. All skull measurements were significantly and positively correlated with PC1, while the correlation between measurements and PC2 and PC3 was positive and negative (all were significant). Thus, differences in female and male skull size was associated with PC1, while PC2 and PC3 separated female and male bears based on differences in skull shape.

Results from the "size-in" and "size-out" CVAs indicated that sexual dimorphism in skull size and shape was greatest in bears from Alberta and least in bears from Newfoundland (Table 4). Size-dependent dimorphism was relatively greater in New York bears than Quebec bears, and shape-dependent dimorphism was relatively greater in the Quebec population than the New York population (Table 4). For bears from Alberta and Newfoundland, differences in skull structure ("size-out" analysis) between sexes was largely due to the second canonical variate (PC3), while differences between female and male bears from Quebec was associated with the first canonical variate (PC2). Both canonical variates appeared equally important in separating female and male bears from New York.

Discussion

Based on the measurements of skull length and breadth used in this study we could not find unequivocal support for our prediction that skull size would be significantly greater in Black Bears from Newfoundland than mainland populations. Newfoundland female skulls were slightly larger than female skulls from New York and significantly larger than individuals from Quebec. Skull size in male bears from Newfoundland was statistically larger than males from Quebec, but similar to males from Alberta and New York. Our prediction was formulated around a recent

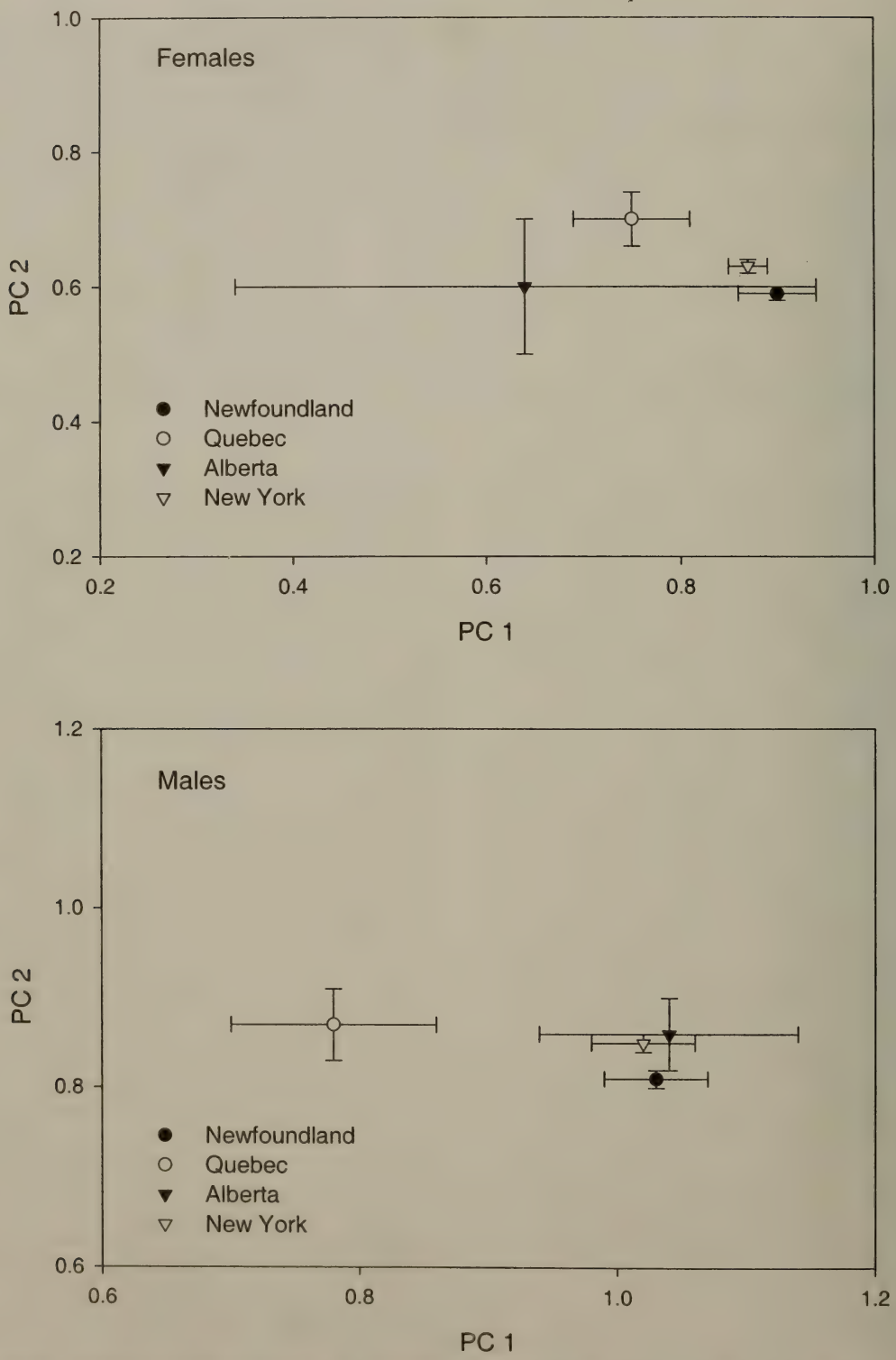


FIGURE 1. Distribution of skull size (PC 1) and shape (PC 2) components for female and male Black Bears from four North American populations. Bars represent 2 SE around the mean.

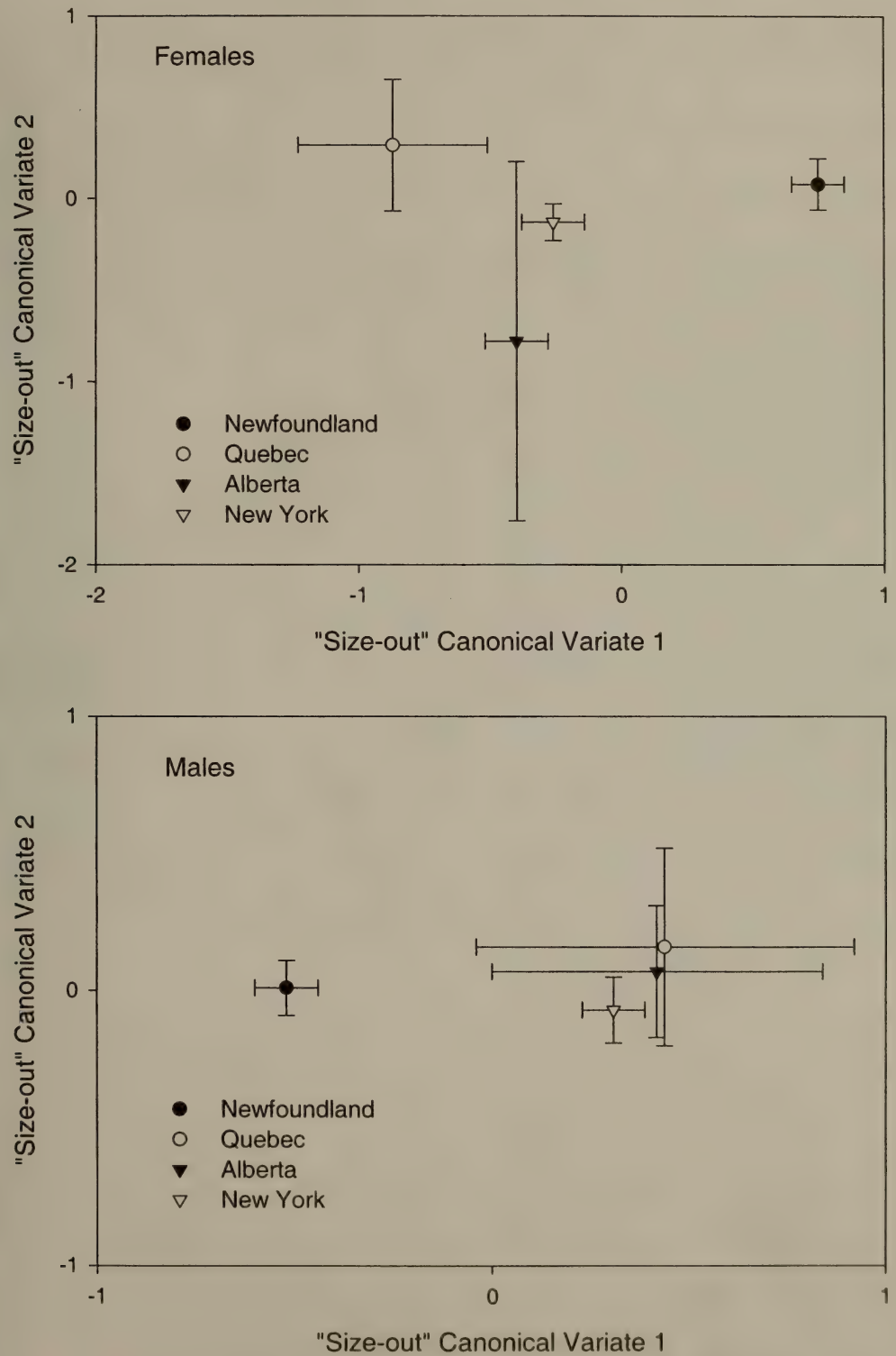


FIGURE 2. Distribution of skull shape ("size-out" analysis) components for female and male Black Bears from four North American populations. Bars represent 2 SE around the mean.

TABLE 4. Indices of degree of sexual dimorphism (SD) for Black Bear populations. Values represent Mahalanobis distances between sexes for an eight-group canonical variate analysis on principal component scores derived from MGPCA.

Population	"Size-in" SD	"Size-out" SD
Alberta	4.03	1.56
Newfoundland	0.41	0.10
New York	0.71	0.33
Quebec	0.61	0.58

analysis of body size in Black Bears (Mahoney et al. 2001), and the assumption that abiotic and biotic environmental selection pressures should exert similar influences on body size and skull size so that the two attributes would exhibit positive covariation.

However, the observed degree of variation in sex-dependent skull size among populations showed little covariance with the amount of variation in body size previously determined for Newfoundland and mainland Black Bear populations (Mahoney et al. 2001). In that analysis, the average relative difference in asymptotic body size between females from the island population and five mainland populations (New Brunswick, Quebec, Ontario, Maine and Alaska) was 55%, while the relative difference between males was 37%. Limited ontogenetic variation in skull size (i.e., between-group variation for PC1 was 6.8% and 7.3% for females and males, respectively) relative to body size variation suggests that selection on skull size is more constrained than body size in North American Black Bears. Because the skull and dentition represent the principal killing apparatus in carnivores, constraints on optimal skull size (and shape) should be strong. However, relative to most freshwater and marine predators, and some reptiles, terrestrial carnivores may be less constrained by gape size (Zaret 1980; DeMarco et al. 1985; Hairston and Hairston 1993; Shine 1996). For solitary terrestrial carnivores, maximum prey size is primarily determined by predator body size (Schoener 1969; Vézina 1985), and theoretically, constraints on selection for local adaptations in body size should be less than skull size. Body size should be able to respond more quickly (i.e., over ecological time), and over a wider range, to changing environmental conditions. We hypothesize that if gape size does not limit prey size in solitary terrestrial carnivores, then large degrees of among-population variation in body size should be coupled with little covariation in skull size. Alternatively, phenotypic variation in body size and skull size may covary among populations or ecotypes, but predicting the direction of covariation between traits may prove difficult (Roff 2000).

After removing ontogenetic effects (i.e., "size-out" analysis), our results clearly showed that skull shape was statistically different in female and male bears from Newfoundland relative to individuals from mainland populations. This pattern is even more striking when one considers the limited number of skull measurements used to separate island and mainland populations of Black Bears in multivariate space. For example, Cameron (1956) examined 12 cranial attributes in 19 Black Bear skulls from eastern Canada to identify bears from Newfoundland as a separate subspecies (*U. a. hamiltoni*). Other studies of North American Brown Bears, European Rabbits (*Oryctolagus cuniculus*), and European Roe Deer (*Capreolus capreolus*) found that skull morphometrics were inadequate for delineating subspecies, and suggested that genetic analysis should be performed to verify taxonomically dissimilar groups (Rausch 1963; Sharples et al. 1996; Aragon et al. 1998). A recent analysis of mitochondrial DNA using eight haplotypes also suggested that Black Bears from Newfoundland represent a separate subspecies from mainland populations, but there was no evidence for a strong phylogenetic split between groups (Paetkau and Strobeck 1996). Thus, it appears that the type of cranial measurements and analysis used here may provide an effective method for distinguishing between potentially different ecotypes of Black Bears across North America.

There are a number of potential abiotic and biotic factors, which are not mutually exclusive, that could be linked to the observed phenotypic variation in size-related skull shape among Black Bear populations. However, without explicit tests of the environmental selection pressures that may be driving between-population variation in skull shape, explanations are purely hypothetical. One factor(s) may be related to spatial and temporal differences in food availability, food items, and/or prey size. Empirical studies have correlated these "food factors" with body size in bears and other predators (Schoener 1969; Case 1978; Ferguson and McLoughlin 2000; Mahoney et al. 2001), but exactly how these elements of diet are related to skull shape is unclear. Variation in cranial shape may also be coupled with historical/current between-population differences in the strength of interspecific competition for food and prey, and subsequent character displacement and (or) release (Abrams 1996; Losos 1996; see Mikulová and Frynta (2001) for history and groups demonstrated). For example, during the past 80 years Black Bears have been the exclusive large carnivore on Newfoundland. Wolves (*Canis lupus*) were extirpated around 1920, and Coyotes (*Canis latrans*) have only inhabited the island since 1985 (Mahoney et al. 2001). Alternatively, phenotypic variation in Black Bear skulls may be the result of a neutral or non-adaptive mutation in the gene complex regulating

cranial shape. Small degrees of variation could have arisen through chance events associated with rapid genetic drift in a small isolated founder population (Paetkau and Strobeck 1996; Slatkin 1996; Lynch et al. 1997).

Similar to the Eurasion Badger (*Meles meles*; Lynch et al. 1997), sexual dimorphism in skull size and shape among Black Bear populations was marginal. Except for the Alberta population (which is likely influenced by small sample size for females), Mahalanobis distances indicated that cranial structure in female and male bears was quite similar. Explanations for the evolution of sexual dimorphism include competitive character displacement, sex-specific differences in partitioning assimilated energy and protein towards somatic tissue growth and reproduction, and sexual selection for increased mating opportunities (Ralls 1977; Ralls and Harvey 1985; Quin et al. 1996; Gittleman and Valkenburgh 1997). But niche separation (character displacement) appears more closely coupled with sexual dimorphism in carnivore species that have a strong preference for animal protein (Ralls and Harvey 1985; Gittleman and Valkenburgh 1997). Although Black Bears are predatory (Mahoney 1986; Schwartz and Franzmann 1991), both female and male Black Bears across North America are sufficiently omnivorous to preclude niche separation as a principal factor driving sexual dimorphism in skull size and shape. For Black Bears, local distribution of prey size and availability, and phenology and dispersion of nutritious plant items is similar for each sex which minimizes the potential for competitive displacement in cranial attributes. While the energetic constraints of reproduction in females would exacerbate sexual dimorphism, we believe that the primary factor responsible for sex-specific differences in skull size in Black Bears is intrasexual selection for increased gape size display in males associated with a polygynous mating system (Bunnel and Tait 1981; Gittleman and Valkenburgh 1997).

Ewer (1973) and Wiig (1986) stipulated that the shape of the carnivore skull is primarily determined by brain size, and jaw and neck musculature (characteristics linked with mastication). If the masticatory apparatus in omnivorous carnivores is under similar selection pressures in both sexes, we should expect little difference in the shape of female and male skulls. Therefore, limited variation in skull shape between females and males may represent a functional adaptation for exploiting the seasonal variation in animal and plant foods available to Black Bears. We recognize, however, that this hypothesis is based on a limited number of skull characteristics and that an analysis using a larger array of cranial attributes may detect a greater degree of sexual dimorphism within and between populations. Thus, although the morphometric measurements used in this study were sufficient for separating Newfoundland and mainland Black Bear ecotypes, a broader suite of skull traits may be necessary for teasing apart any potential functional differences in cranial shape between female and male bears.

Acknowledgments

We thank the many staff of the Newfoundland and Labrador Wildlife Division, and the personnel from Gros Morne National Park and Terra Nova National Park. Our greatest appreciation is extended to the following people and government agencies who provided skull morphology data: L. Berchielli with the Wildlife Research Center, New York; H. Jolicoeur with the Government of Quebec, and J. R. Gunson with Alberta Environmental Protection, Fish and Wildlife Division. We benefited from the constructive comments of B. McLaren and T. Miller. We are extremely grateful for the statistical expertise and analysis provided by Dr. John M. Lynch (Arizona State University). Funding for this project was provided by the provincial government of Newfoundland and Labrador who have continued their commitment to the development of wildlife science.

Literature Cited

Abrams, P. A. 1996. Evolution and the consequences of species introductions and deletions. Ecology 77: 1321-1328.

Aragon, S., F. Braza, C. S. Jose, and **P. Fandos.** 1998. Variation in skull morphology of roe deer (*Capreolus capreolus*) in western and central Europe. Journal of Mammalogy 79: 131-140.

Armbruster, W. S., and **K. E. Schwaegerle.** 1996. Causes of covariation of phenotypic traits among populations. Journal of Evolutionary Biology 9: 261-276.

Arnold, S. J. 1992. Constraints on phenotypic evolution. American Naturalist 140: S85-S107.

Bunnel, F. L., and **D. E. N. Tait.** 1981. Population dynamics of bears – implications. Pages 75-98 *in* Dynamics of large mammal populations. *Edited by* C. W. Fowler and T. D. Smith. John Wiley & Sons, New York, NY.

Cameron, A. W. 1956. A new black bear from Newfoundland. Journal of Mammalogy 37: 538-540.

Case, T. J. 1978. A general explanation for insular body size in terrestrial vertebrates. Ecology 59: 1-18.

Chestin, I. E., and **N. G. Mikeshina.** 1998. Variation in skull morphology of brown bears (*Ursus arctos*) from Caucasus. Journal of Mammalogy 79: 118-130.

DeMarco, V. G., R. W. Drenner, and **G. W. Ferguson.** 1985. Maximum prey size of an insectivorous lizard (*Sceloporus undulatus garmani*). Copeia 1985: 1077-1080.

Ewer, R. F. 1973. The carnivores. Weidenfeld and Nicholson, London, UK.

Felsenstein, J. 1988. Phylogenies and quantitative characters. Annual Review of Ecology and Systematics 19: 445-471.

Ferguson, S. H., and **P. D. McLoughlin.** 2000. Effect of energy availability, seasonality, and geographic range on brown bear life history. Ecography 23: 193-200.

Gittleman, J. L., and **B. Valkenburgh.** 1997. Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology. Journal of Zoology (London) 242: 97-117.

Hairston, N. G., Jr, and **N. G. Hairston.** 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. American Naturalist 142: 379-411.

Harvey, P. H., and **G. M. Mace.** 1982. Comparisons between taxa and adaptive trends: problems and methodology. Pages 343-361 *in* Current problems in sociobiology. *Edited by* Kings College Sociobiology Group. Cambridge University Press, Cambridge, U.K.

Lande, R. 1982. A quantitative genetic theory of life history evolution. Ecology 63: 607-615.

Losos, J. B. 1996. Phylogenetic perspectives on community ecology. Ecology 77: 1344-1354.

Lynch, J. M., and **T. J. Hayden.** 1995. Genetic influences on cranial form: variation among ranch and feral American mink *Mustela vison* (Mammalia: Mustelidae). Biological Journal of the Linnaean Society 55: 293-307.

Lynch, J. M., J. W. H. Conroy, A. C. Kitchener, D. J. Jefferies, and **T. J. Hayden.** 1996. Variation in cranial form and sexual dimorphism among five European populations of otter *Lutra lutra* (L.). Journal of Zoology (London) 238: 81-96.

Lynch, J. M., R. Whelan, A. I. Il. Fituri, and **T. J. Hayden.** 1997. Craniometric variation in the Eurasian badger (*Meles meles*). Journal of Zoology (London) 242: 31-44.

Mahoney, S. P. 1986. The black bear in Newfoundland. Osprey 16: 10-21.

Mahoney, S. P., J. A. Virgl, and **K. Mawhinney.** 2001. Potential mechanisms for the phenotypic divergence in body size between Newfoundland and mainland black bear populations. Canadian Journal of Zoology 79: 1650-1660.

Mikulová, P., and **D. Frynta.** 2001. Test of character displacement in urban populations of *Apodemus sylvaticus*. Canadian Journal of Zoology 79: 794-801.

Paetkau, D., and **C. Strobeck.** 1996. Mitochondrial DNA and the phylogeography of Newfoundland black bears. Canadian Journal of Zoology 74: 192-196.

Quin, D. G., A. P. Smith, and **T. W. Norton.** 1996. Ecogeographic variation in size and sexual dimorphism in sugar gliders and squirrel gliders (Marsupialia: Petauridae). Australian Journal of Zoology 44: 19-45.

Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. American Naturalist 111: 917-938.

Ralls, K., and **P. H. Harvey.** 1985. Geographic variation in size and sexual dimorphism of North American weasels. Biological Journal of the Linnaean Society 25: 119-167.

Rausch, R. L. 1963. Geographic variation in size in North American brown bears (*Ursus arctos*) as indicated by condylobasal length. Canadian Journal of Zoology 41: 33-45.

Roff, D. A. 2000. Trade-offs between growth and reproduction: an analysis of the quantitative genetic evidence. Journal of Evolutionary Biology 13: 434-445.

Schoener, T. W. 1969. Models of optimal size for solitary predators. American Naturalist 103: 277-313.

Schwartz, C. C., and **A. W. Franzmann.** 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs 113: 1-58.

Sharples, C. M., J. M. Fa, and **D. J. Bell.** 1996. Geographical variation in size in the European rabbit (*Oryctolagus cuniculus*, Lagamorpha: Leporidae) in western Europe and North America. Zoological Journal of the Linnaean Society 117: 141-158.

Shine, R. 1996. Life history evolution in Australian snakes: a path analysis. Oecologia 107: 484-489.

Slatkin, M. 1996. In defense of founder-flush theories of speciation. American Naturalist 147: 493-505.

Thorpe, R. S. 1988. Multiple group principal component analysis and population differentiation. Journal of Zoology (London) 216: 37-40.

Vézina, A. F. 1985. Empirical relationships between predator and prey size among terrestrial vertebrate predators. Oecologia 67: 555-565.

Wiig, O. 1986. Sexual dimorphism in the skull of minks, *Mustela vison*, badgers, *Meles meles*, and otters, *Lutra lutra*. Zoological Journal of the Linnean Society 87: 163-179.

Wiig, O. 1989. Craniometric variation in Norwegian wolverines (*Gulo gulo*). Zoological Journal of the Linnaean Society 95: 177-204.

Wiig, O. 1992. Carnivore morphometrics: a study of skull variation and its significance. Ph.D. thesis. Zoological Museum, University of Bergen.

Wiig, O, and **T. Andersen.** 1986. Sexual size dimorphism in the skull of Norwegian lynx. Acta Theriologica 31: 147-155.

Willey, C. H. 1974. Aging black bears from first premolar tooth sections. Journal of Wildlife Management 38: 97-100.

Zaret, T. M. 1980. Predation and freshwater communities. Yale University Press, New Haven.

Received 14 January 2002
Accepted 1 December 2003

Food Habits of Ermine, *Mustela erminea*, in a Forested Landscape

MARK A. EDWARDS[1] AND GRAHAM J. FORBES

University of New Brunswick, N.B. Cooperative Fish & Wildlife Research Unit, Fredericton, New Brunswick E3B 6C2 Canada

[1]Present address: University of Alberta, Department of Biological Sciences, Biological Sciences Building, Edmonton, Alberta T6G 2E9 Canada

Edwards, Mark A., and Graham J. Forbes. 2003. Food habits of Ermine, *Mustela erminea*, in a forested landscape. Canadian Field-Naturalist 117(2): 245-248.

Most research pertaining to the diet of North American weasels has been conducted in agricultural areas and may not be representative of diets in forested regions. Ermine carcasses (N = 155) collected from trappers during a two-week harvest (16-30 November 1996) in forested New Brunswick were analyzed for food habits. The contents of 81 stomachs and 98 gastrointestinal tracts (N = 179) were considered as separate eating events and used in the calculation of the percent frequency of occurrence. Results suggest that soricids (28.0%), arvicolines (24.6%), and cricetines (17.3%) comprised two-thirds of their autumn diet. At a species or genus level, the Deer Mouse (*Peromyscus maniculatus*) (17.3%) and shrews (*Sorex* spp.) (28.0%) were shown to have the highest percent occurrence. Squirrels, including the Red Squirrel (*Tamiasciurus hudsonicus*) and the Eastern Chipmunk (*Tamius striatus*), comprised 11.2% of the Ermine's diet; a value higher than has previously been reported.

Key Words: Ermine, *Mustela erminea*, Long-Tailed Weasel, *Mustela frenata*, food habits, diet analysis, forest landscape.

Though a common predator in most forested landscapes, we were able to locate few studies on weasel (*Mustela* spp.) food habits in forested landscapes but numerous studies in agricultural landscapes (i.e., review in King 1990). Weasel species such as the Ermine (*Mustela erminea*) are found in fields and forests throughout the Holarctic but there are risks associated with extrapolating food habits from agricultural landscapes to forested landscapes when the availability of prey species and size differs markedly between landscapes.

Most of the literature pertaining to the Ermine indicates many species, but in particular voles, are the Ermine's principal prey (Erlinge 1983; King 1990; Hanski et al. 1991). Arvicolines (e.g., voles, lemmings) dominate consumed prey species to the extent that Ermine are considered specialist predators of voles (Simms 1979; Nams 1980; King 1990). However, this conclusion is based on studies conducted in primarily agricultural (Erlinge 1975, 1981, 1983; Raymond et al. 1984; King 1990; Oksanen and Schneider 1995), Low Arctic (Maher 1967; McLean et al. 1974), and Arctic landscapes (Simms 1978).

For studies conducted in forest-dominated landscapes prey representation is similar to studies conducted in agriculturally dominated landscapes; however, prey consumption can vary. In field-dominated landscapes, Ermine selected voles over other prey types (Simms 1979; Raymond et al. 1984; Derting 1989). This may not be true in forested landscapes where the availability of larger prey species (i.e., sciurids) and the ability to capture prey differs because of vertical structures and debris that offer different escape strategies of small mammals. In a series of trials conducted in enclosures, Derting (1989) reported that Least Weasels (*Mustela nivalis*) demonstrated an opportunistic foraging behaviour and attacked all prey offered. However, differences in escape tactics resulted in voles (*Microtus* spp.) being captured more frequently. In the presence of a weasel, voles responded by running and were quickly caught and killed, whereas Field Mice (*Apodemus sylvaticus*) made rapid and erratic escape movements and evaded capture by climbing upward and freezing (Erlinge 1975; Derting 1989; King 1990).

In forest habitats, Ermine are able to hunt in the space created by ericaceous shrubs and woody debris (Simms 1979; Edwards et al. 2001). Simms (1979) suggested that in areas where resource partitioning exists between sympatric predators, as in the boreal forest, Deer Mice might be the Ermine's most frequent prey choice. Higher availability, and habitat characterized by the presence of mosses and ericaceous shrubs carpeting the forest floor might make the Deer Mouse easier to catch. Instead of freezing and/or climbing (Erlinge 1975; Derting 1989; King 1990), Deer Mice in these regions may alter escape tactics and escape into the spaces created by mosses and shrubs, where weasels can follow with success (Simms 1979).

Our objective was to document the food habits of a common and widespread weasel species in a forest-dominated landscape to gain a better understanding of the impact weasels have on small mammal populations in forested landscapes. To do this we compared our results with other forest-based studies on weasel food habits.

Methods

Trappers submitted a total of 165 weasels during the 1996 province-wide New Brunswick harvest (16-

30 November). New Brunswick is >85% forested (Natural Resources Canada 2000) and weasels are trapped in forests along the same trap lines used by trappers for Marten (*Martes americana*) trapping (C. Libby, personal communication). Skull (N=142) and body (weight, length of body, tail, hind foot) measurements were made to separate Ermine from Long-Tailed Weasel (*M. frenata*), an uncommon species in New Brunswick (Dilworth 1984).

The stomach of an Ermine has a maximum capacity of 10 to 20 g and it is unlikely that they can consume more than the equivalent of one small rodent at one time (King 1990). Gilligham (1984) reported that the Least Weasel cannot eat more than a few grams at one time and no more than one meal within a few hours. Therefore, a single stomach or intestine will generally contain only one item (Aldous and Manweiler 1942; Heidt 1972; Simms 1978; McDonald et al. 2000). The contents of the stomach and gastro-intestinal (GI) tract constitute one meal each, consumed at separate time intervals. This allowed for two samples to be collected from each individual.

The contents of each stomach and GI tract were removed, rinsed separately in a plastic container, and then washed through a 35-grade sieve. The remaining stomach or GI tract contents were viewed through a dissecting microscope and identifiable items removed. Flesh was not identified and vegetable matter was assumed to be incidental (Erlinge 1975; Simms 1978). Hairs were imprinted on a slide treated with hair spray and identified using a compound microscope. A reference collection of study skins and various keys (Day 1966; Adorjan and Kolenosky 1969; Thompson et al. 1987) facilitated identification of prey remains. All mammalian prey was identified to species, except *Microtus* spp. and *Sorex* spp., which are difficult to identify beyond the genus level (Thompson et al. 1987). Attempts were not made to identify microscopic invertebrate remains and woody debris since such materials were considered incidental (King 1990; McDonald et al. 2000). The frequency of occurrence for each food item in the diet was determined by counting the number of times each item occurred in the total sample of stomachs and GI tracts. The percent frequency of occurrence was presented as the total percentage of prey items in the sample. This method was appropriate for reporting the diet of Ermine because it identified the smallest number of consumed prey items (McDonald et al. 2000). Empty stomachs and GI tracts were not included in the analysis.

Availability of prey was not known since the sample originated from throughout the province of New Brunswick. The most abundant shrew species available are the Short-Tailed (*Blarina brevicauda*), and the Masked Shrew (*Sorex cinereus*) (Dilworth 1984; G. Forbes, unpublished data). The common vole species in forest landscapes is the Red-Backed Vole (*Clethrionomys gapperi*) while the Yellow-Nosed (*Microtus chrotorrhinus*) and the Meadow Vole (*M. pennsylvanicus*) are relatively rare (Bowman 2001). The Deer Mouse (*Peromyscus maniculatus*) is common. The Red Squirrel (*Tamiasciurus hudsonicus*) and the Snowshoe Hare (*Lepus americana*) are common throughout the province.

Results

A collection of 165 weasel carcasses resulted in 155 (93.9%) Ermine and 10 (6.1%) Long-Tailed Weasels. Only Ermine were included in the analysis. The sex ratio was 141 (91.0%) males to 14 (9.0%) females. Seventy-four stomachs (47.7%) and 57 GI tracts (36.8%) were found to be empty and excluded from the analysis. The resulting sample included 81 stomachs and 98 GI tracts (N= 179). Species were grouped into eight categories based on taxonomic association: voles and lemmings (Microtinae), mice (Cricetidae), shrews (Soricidae), squirrels (Sciuridae), weasels (Mustelidae), feathers, other fauna, and unknown (Table 1). The category "other fauna" included prey items where the frequency of occurrence was ≤ 2.

The most commonly consumed were the Deer Mouse and *Sorex* species (likely *Sorex cinereus* because of its abundant status), and smaller amounts of several species of arvicolines (Table 1). In terms of taxonomic groupings, weasels preyed on roughly equal amounts of each group. Arvicolines comprised 24.6% of total prey while Cricetines (Deer Mice) comprised 17.3%. Shrews comprised 28.0% of the prey items. Two sciurids, Eastern Red Squirrel at 8.4% and Eastern Chipmunk (*Tamia striatus*) at 2.8% comprised 11.2% of total items. Feathers made up 5.0% of the total prey items.

Discussion

It is difficult to compare studies on weasel diet because prey proportions are dependent on the gender of the weasel, regional characteristics and prey availability (Aldous and Manweiler 1942; Simms 1978; Whitaker and French 1984). We compare only North American-based studies because Ermine body size varies greatly between continents (Banfield 1974; King 1990). Studies in either agricultural and forest landscapes, however, have comparable prey representation; deer mice (*Peromyscus* spp.) are found in forest woodlots, old fields and edges of agricultural-dominated landscapes (Banfield 1974; Dilworth 1984). Voles (*Microtus* or *Clethrionomys* spp.) are present in a range of forest and field habitat. We note that our sample was collected in late fall when Woodland Jumping Mice (*Napaeozapus insignis*) are inactive due to hibernation.

Although studies conducted in primarily agricultural areas have indicated voles are the weasel's principal prey (Erlinge 1975), our results indicated that mice and shrews are preyed on more heavily in forests. These results are similar to what Simms (1979) found in the forests of Algonquin Park. If we focus on a

TABLE 1. Diet of 155 Short-tailed Weasels trapped during the fall season (16-30 November, 1996) in New Brunswick, expressed as frequency of occurrence (N=179), and percent of occurrence.

Prey type	Frequency of Occurrence	Percent of Occurrence
Voles and Lemmings		
Clethrionomys gapperi	15	8.4
Microtus spp.	17	9.5
Synaptomys cooperi	12	6.7
Mice		
Peromyscus maniculatus	31	17.3
Shrews		
Blarina brevicauda	8	4.5
Sorex spp.	42	23.5
Squirrels		
Tamiasciurus hudsonicus	15	8.4
Tamius striatus	5	2.8
Weasels		
Mustela sp.	11	6.1
Feathers	9	5.0
Other fauna	5	2.8
Unknown	9	5.0
Total	179	100.0

single species, Deer Mice appear to be the most preyed upon species, suggesting in our study that weasels are not simply specialists of voles. We suggest that Ermine feeding habits should be defined by the relative abundance and availability of prey with different escape tactics (Aldous and Manweiler 1942; Erlinge 1975; Raymond et al. 1984; Derting 1989). Voles generally run from weasels and Deer Mice remain still after climbing. Shrews are more aggressive and require more energy to subdue (Vaudry et al. 1990). Based on a grouping of these types of behaviour, Ermine in forest landscapes appear to feed almost equally among these behaviours. This suggests a semi-generalist opportunistic feeding strategy by Ermine.

The carcasses used in this study were dominated by males. This is a common bias in trapping because body size, trap geometry and gender specific behaviour make males more susceptible to trapping (Buskirk and Lindstedt 1989). Squirrel remains were recorded in higher proportions than have previously been reported for Ermine (Aldous and Manweiler 1942; Simms 1979). The high ratio of males to females in our sample and the more opportunistic foraging behaviour of larger male weasels (Raymond et al. 1984; Derting 1989; Murphy et al. 1998) may explain the higher abundance of squirrels. Larger subspecies of *M. erminea* feed on larger prey but the subspecies in New Brunswick is comparatively small (King 1990). Evidence of feeding on Snowshoe Hare, an even larger potential prey, was not found in our study. Larger male weasels would be able to exploit larger, more aggressive prey items, like squirrels and Snowshoe Hare, which would require a higher risk of injury and higher energy expenditure (Erlinge 1975; Raymond et al. 1984; Vaudry et al. 1990). McDonald et al. (2000) found that female Stoats preyed primarily on small mammals, and male Stoats ate higher numbers of large prey items. Thompson and Colgan (1990) suggested that smaller prey requiring minimal energy costs may be taken incidentally by Marten, a larger mustelid species, while searching for larger prey items. The average biomass of a shrew is approximately half of a cricetine and quarter that of an arvicoline. Although larger prey items occur less frequently in the diet of small carnivores like the weasel, they might be more important in terms of caloric intake (Cumberland et al. 2001). The average biomass of a squirrel is approximately seven times greater than a cricetine and four times greater than an arvicoline (Dilworth 1984).

These results support research that, at a species level, shows Deer Mice and shrews (*S. cinereus*) occur more frequently than voles in the diets of weasels from forested landscapes than from agricultural and agro-forested regions. As a group voles are consumed in near-equal amounts as shrews and mice. Combined, these results do not support the notion that Ermine are vole-feeding specialists. Rather, Ermine seem to be able to prey on a range of species, implying a semi-generalist and opportunistic feeding strategy. The availability in forests of prey items of larger biomass such as squirrels could give an advantage over grassland systems where the ability to predate larger prey like the Woodchuck (*Marmota monax*), the largest and most aggressive ground-squirrel species and the only one found in New Brunswick (Dilworth 1984), is minimal. Alternatively, more food per effort obtained from squirrels may offset the energy required to pursue prey in the maze of debris found on the forest

floor. Further research on the energetic costs of pursuing a range of prey body-sizes and escape tactics in a structurally complex environment is required.

Acknowledgment

We are grateful for the assistance of the New Brunswick Trappers Association and the New Brunswick Department of Natural Resources and Energy for providing samples. We thank Cade Libby, New Brunswick Furbearer Biologist, Fredericton, N.B., for the information on ermine trapping in New Brunswick. We would also like to thank the Sustainable Forest Management Network of Centres of Excellence and the University of New Brunswick. Two anonymous reviewers contributed to the text.

Literature Cited

Adorjan, A. S., and **G. B. Kolenosky**. 1969. A manual for the identification of hairs of selected Ontario mammals. Department of Lands and Forests. Ontario Research Report 90. Ottawa, Ontario, Canada.

Aldous, S. E., and **J. Manweiler**. 1942. The winter food habits of the short-tailed weasel in northern Minnesota. Journal of Mammalogy 23: 250-255.

Banfield, A. W. F. 1974. The mammals of Canada. University of Toronto Press, Toronto, Ontario, Canada. 438 pages.

Buskirk, S. W., and **S. L. Lindstedt.** 1989. Sex biases in trapped samples of mustelidae. Journal of Mammalogy 70: 88-97.

Bowman, J., G. Forbes, and **T. Dilworth**. 2001. Landscape context and small-mammal abundance in a managed forest. Forest Ecology and Management 140: 249-255

Cumberland, R., J. Dempsey, and G. Forbes. 2001. Should food habits be based on biomass? Importance of large prey to the American marten. Wildlife Society Bulletin 29: 1125-1130.

Day, M. G. 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. Journal of Zoology 148: 201-217.

Derting, T. L. 1989. Prey selection and foraging characteristics of least weasels (*Mustela nivalis*) in the laboratory. American Midland Naturalist 122: 394-400.

Dilworth, T. G. 1984. Land Mammals of New Brunswick. T. G. Dilworth, Fredericton, New Brunswick, Canada.

Edwards, M. A., G. J. Forbes, and **J. Bowman**. 2001. Fractal dimension of ermine, *Mustela erminea* (Carnivora: Mustelidae), movement patterns as an indicator of resource use. Mammalia 65: 220-225.

Erlinge, S. 1975. Feeding habits of the weasel *Mustela nivalis* in relation to prey abundance. Oikos 26: 378-384.

Erlinge, S. 1981. Food preference, optimal diet and reproduction output in stoats *Mustela erminea* in Sweden. Oikos 36: 303-315.

Erlinge, S. 1983. Demography and dynamics of a stoat *Mustela erminea* population in a diverse community of vertebrates. Journal of Animal Ecology 52: 705-726.

Gamberg, M., and **J. L. Atkinson**. 1988. Prey hair and bone recovery in ermine scats. Journal of Wildlife Management 52: 657-660.

Gilligham, B. J. 1984. Meal size and feeding rate in the least weasel (*Mustela nivalis*). Journal of Mammalogy 65: 517-519.

Hanski, I., L. Hansson, and **H. Henttonen**. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. Journal of Animal Ecology 60: 353-367.

Heidt, G. A. 1972. Anotomical and behavioural aspects of killing and feeding by the least weasel *Mustela nivalis* L. Arkansas Academy of Science Proceedings 26: 53-54.

King, C. 1990. The natural history of weasels and stoats. Cornell University Press, Ithaca, New York, USA. 253 pages.

Maher, W. J. 1967. Predation by weasels on a winter population of lemmings, Banks Island, Northwest Territories. Canadian Field-Naturalist 81: 248-250.

McDonald, R. A., **C. Webbon**, and **S. Harris**. 2000. The diet of stoats (*Mustela erminea*) and weasels (*Mustela nivalis*) in Great Britain. Journal of Zoology (London) 252: 363-371.

McLean, S. F., Jr., B. M. Fitzgerald, and **F. A. Pitelka**. 1974. Population cycles in Arctic lemmings: winter reproduction and predation by weasels. Arctic and Alpine Research 6: 1-12.

Murphy, E. C., B. K. Clapperton, P. M. F. Bradfield, and **H. J. Speed**.1998. Effects of rat-poisoning operations on abundance and diet of mustelids in New Zealand podocarp forests. New Zealand Journal of Zoology 25: 315-328.

Nams, V. 1980. Prey selection mechanisms of the ermine (*Mustela erminea*). Pages 861–882 *in* Worldwide Furbearer Conference Proceedings. *Edited by* J. A Chapman and D. Pursley. Frostburg Worldwide Furbearer Conference Inc., Maryland, USA.

Natural Resources Canada. 2000. State of Canada's Forests 1999-2000. Natural Resources Canada, Ottawa, Ontario, Canada. 121 pages.

Oksanen, T., and **M. Schneider**. 1995. The influence of habitat heterogeneity on predator-prey dynamics. Pages 122–150 *in* Landscape Approaches in Mammalian Ecology and Conservation. *Edited by* W. Z. Lidicker. University of Minnesota Press, Minnesota, USA.

Raymond, M. J. , M. Bergeron and **Y. Plates**. 1984. Dimorphisme sexuel et regime alimentaire de l'hermine dans un agrosysteme du Québec. Canadian Journal of Zoology 62: 594-600.

Simms, D. A. 1978. Spring and summer food habits of an ermine (*Mustela erminea*) in the central Arctic. Canadian Field-Naturalist 92: 192-193.

Simms, D. A. 1979. North American weasels: resource utilization and distribution. Canadian Journal of Zoology 57: 504-520.

Thompson, I. D., and **P. W. Colgan**. 1990. Prey choice by marten during a decline in prey abundance. Oecologia 83: 443-451.

Thompson, I. D., M. Porter, and **S. L. Walker**. 1987. A key to the identification of some small boreal mammals of central Canada from guard hairs. Canadian Field-Naturalist 101: 614-616.

Vaudry, R., M. Raymond, and **J. F. Robitaille**. 1990. The capture of voles and shrews by male and female ermine *Mustela erminea* in captivity. Holarctic Ecology 13: 265-268.

Whitaker, J. O., Jr., and **T. W. French**. 1984. Foods of six species of sympatric shrews from New Brunswick. Canadian Journal of Zoology 62: 622-626.

Received 25 February 2002
Accepted 3 November 2003

Distribution and Conservation of the Harlequin Duck, *Histrionicus histrionicus*, in Greenland

David Boertmann

National Environmental Research Institute, Department of Arctic Environment, P.O. Box 358, DK-4000 Roskilde, Denmark

Boertmann, David. 2003. Distribution and conservation of the Harlequin Duck, *Histrionicus histrionicus*, in Greenland. Canadian Field-Naturalist 117(2): 249-256.

The breeding range of the Harlequin Duck (*Histrionicus histrionicus*) in Greenland includes West Greenland to as far north as 72° 30' N and a few sites in East Greenland. The breeding population is guessed at a few thousand pairs. During winter Harlequin Ducks occur along the West Greenland coast between Maniitsoq and Nanortalik. The size of the winter population is unknown. As Canadian males, which have moulted in Southwest Greenland, also winter there, perhaps accompanied by females and juveniles, the numbers may be considerable. The peak period for clutch initiation seems to be mid- to late June. There is no immediate conservation concern for the small breeding population of Harlequin Ducks in Greenland. However, there is a risk from marine oil spills along coasts where congregations of non-breeding Harlequin Ducks from both Greenland and eastern Canada occur.

Key Words: Harlequin Duck, *Histrionicus histrionicus*, Greenland, breeding status, winter status, conservation, threats, local use.

Within the Atlantic range of the Harlequin Duck (*Histrionicus histrionicus*) there are three disjunct breeding areas: Iceland, Greenland, and eastern Canada (Boertmann 1994; Robertson and Goudie 1999; Petersen 2000). The breeding populations in these three areas are apparently small, but the size has been estimated only for Iceland with 2000-3000 pairs (Petersen 1998). The non-breeding range includes the Atlantic coasts of Iceland, Southwest Greenland and Canada/USA between Newfoundland and Maryland (Vickery 1988; Boertmann 1994; Robertson and Goudie 1999; Petersen 2000). Compared to the apparently hundreds of thousands of non-breeding Harlequin Ducks along the Pacific coasts of North America (see Robertson and Goudie 1999), the known numbers in the North Atlantic are two orders of magnitude lower; for example, only 1800 birds were recently estimated to winter in eastern North America (Mittelhauser 2000*).

The eastern Canadian population is considered endangered (Goudie 1991). It was recently discovered that males from that population migrate to moulting grounds in West Greenland (Brodeur et al. 1999a, 1999b*, 2002). This discovery, in combination with the results of an aerial survey of moulting Harlequin Ducks in July 1999 in West Greenland (Boertmann and Mosbech 2002), suggests that an update of the species' occurrence in Greenland would be desirable. Previous knowledge on this occurrence was published in several more or less comprehensive works (Oldenow 1933; Salomonsen 1950, 1967, 1974, 1981; Boertmann 1994). The updated information on breeding and winter occurrence is summarised here, while information on moulting birds in Greenland was reported by Boertmann and Mosbech (2002).

Material

At the Zoological Museum of Copenhagen (ZMUC) 194 Greenland specimens of Harlequin Ducks were studied in order to determine phenology, breeding and winter distribution, etc. Of these, eight chicks (Table 1) and 155 full-grown individuals (Table 2) are adequately labelled to be included in the present analysis. Additional information was derived from ZMUC's egg-collection (Table 2) and bird-banding files. However, only ten Harlequin Ducks have been banded in Greenland, all in the period 1946-1969 (Salomonsen 1979). Historical and local information was compiled from the literature, inquiries of people in Greenland and the extensive correspondence of the late Finn Salomonsen (in ZMUC). Finally, opportunistic observations of Harlequin Ducks made during surveys and fieldwork by other biologists and myself in Greenland since 1985 are included. Locations and areas mentioned in the text are indicated on the map (Figure 1).

Results

In West Greenland, breeding has been confirmed only 23 times at 18 different sites (Table 1). At 19 other sites birds have been recorded in similar habitats, but without definite proof of breeding (Table 1). In West Greenland breeding and potential breeding records are distributed from Nanortalik District at 60° N to southern Upernavik District at 72° 30' N (Figure 1). Half the breeding and potential breeding records are from Paamiut, Nuuk and southern Maniitsoq Districts. In East Greenland breeding has been proven at two sites (Figure 1): in the extreme south (Knudsen 1935) and near Tasiilaq Town (Helms 1926). In 1992 a pair was observed near Skjoldungen, between those two

TABLE 1. Observations of breeding and potentially breeding Harlequin Ducks in Greenland.

Date	Type	District	N lat.	Elevation	Source
Confirmed breeding records					
Unknown, before 1920	Nest found	Uummannaq	71°	unknown	Bertelsen 1921
Unknown ca. 1980	female with chicks	Sismiut	67°	<50 m asl	O. Vognsen pers. comm.
6 June 1902	6 eggs	Nuuk	64°	unknown	ZMUC
23 June 1900	4 eggs	Nuuk	64°	unknown	ZMUC
27 June 1927	7 eggs	Nuuk	64°	unknown	ZMUC
4 July 1879	1 egg	Uummannaq	71° 30'	unknown	ZMUC
9 July 1974	5 newly hatched chicks	Paamiut	61°	<100 m asl	Boertmann 1979
24 July 1926	6 chicks, age unspecified	Tasiilaq	60°	unknown	Knudsen 1935
Late July 2001	2 clutches, 4 and 7 chicks	Nuuk [b]	64°	at sea	F. Wille pers. comm.
August 1879	2 chicks < 1 week old	Disko Island	69°	unknown	ZMUC
1 August 1947	2 chicks ringed	Nuuk	64° 30'	<50 m asl	ZMUC
3 August 1950	1 chick ringed	Uummannaq [a]	71° 30'	< 50 m	ZMUC
14 August 1905	small chick	Tasiilaq	66° 45'	unknown	Helms 1926
16 August 1955	6 chicks ringed	Uummannaq [a]	71° 30'	<50 m	ZMUC
19 August 1970	5 chicks	Upernavik	72° 30'	<50 m	E. Isakson in litt.
23 August 1919	4 chicks, < 1 week old	Maniitsoq	66° 30'	unknown	ZMUC
Late August 2001	3 large chicks	Nanortalik	61°	<100 m asl	B. Persson in litt.
3 September 2003	2 chicks	Nuuk [b]	64°	sea level	K.E. Kleist in litt.
5 September 1989	3 large chicks	Uummannaq [a]	71° 30'	at sea	Bennike 1990
8 September 1893	1 large chick, nearly fledged	Paamiut	62°	unknown	ZMUC
10 September 1918	1 chick, 1-2 weeks old	Maniitsoq	66° 30'	unknown	ZMUC
12 September 1904	4 large chicks, not yet fledged	Tasiilaq	66° 45'	unknown	Helms 1926
19 September 2003	1 large chick, not yet fledged	Disko Island	70°	at sea	A. Mosbech pers. comm.
Potential breeding records					
6 June 1978	2 pairs at river	Disko Island	69°	sea level	Kampp and Kristensen 1980*
1960-1970	Pairs seen regularly	Sisimiut	67°	sea level	P. Grossmann pers. comm.
1985	3 or 4 pairs at river	Maniitsoq	66° 30'	50 m asl	Secher et al. 1987
5 July 1992	Pair at river	Maniitsoq	65°	sea level	own observation
1996	Pair at river	Maniitsoq	65°	100 m asl	P. Aastrup pers. comm.
May 1954	Pair	Nuuk	64°	unknown	ZMUC
1990	2 or 3 pairs at river	Nuuk	64°	250 m asl	P. Aastrup pers. comm.
1990	Pairs seen regularly at river	Nuuk	64°	300 m asl	P. Aastrup pers. comm.
28 June 2003	1 male and 5 females on river	Nuuk	63°	sea level	L. Vilhelmsen pers. comm.
1990-1998	Pairs seen regularly at river	Paamiut	62°	<100 m asl	B. Knudsen pers. comm.
1995	Pair seen at river	Paamiut	62°	<150 m asl	B. Knudsen pers. comm.
1990-1998	Pair seen regularly at river	Paamiut	62°	<150 m asl	B. Knudsen pers. comm.
20 June 1985	5 pairs at river mouth	Paamiut	61° 30'	sea level	own observation
23 June 1985	2 pairs at river	Paamiut	61° 30'	25 m asl	own observation
1988-1999	Several pairs at river mouth	Paamiut	61°	sea level	several sources [c]
1988	Pairs at river mouth	Paamiut	61°	sea level	F. Wille pers. comm.
12 June 1935	Pair shot	Narsaq	61°	unknown	ZMUC
20 May 1908	Male shot	Nanortalik	60°	unknown	ZMUC
31 July 1992	Pair seen	Tasiilaq	63° 30'	sea level	J. Rosing pers. comm.

[a] same locality, [b] same locality, [c] K. Kampp personal communication, B. Knudsen personal communication, F. Wille personal communication.

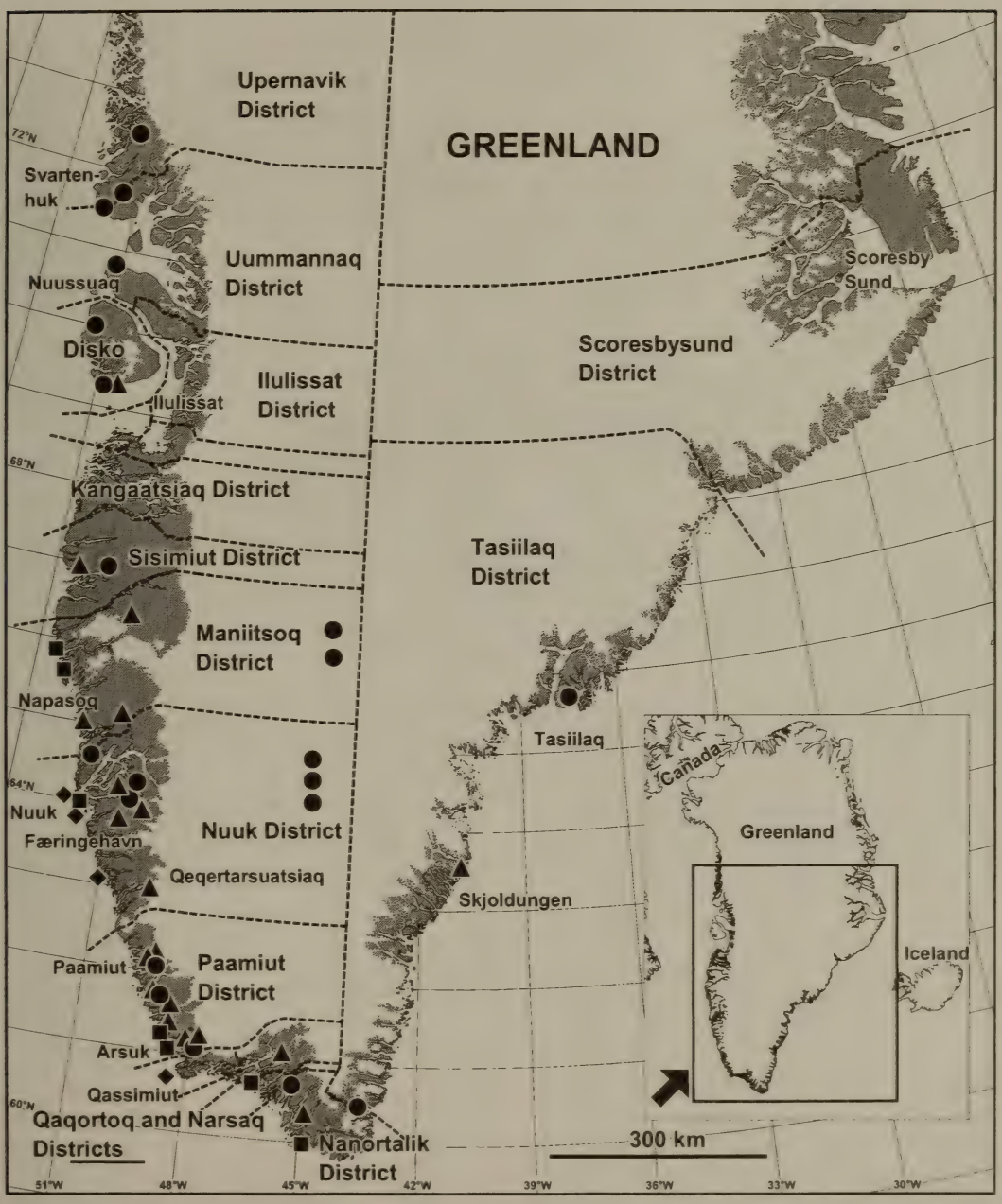


FIGURE 1. Distribution of breeding, probable breeding and winter records of Harlequin Ducks in Greenland: 1= confirmed breeding records (dots placed to the right (on the Inland Ice), represent records which only can be located to a district.), s = records from potential breeding habitats, n = winter records from the literature, local knowledge and the skin collection in Zoological Museum, Copenhagen, u = winter records made during surveys for Common Eider, *Somateria mollissima*, in March 1999 (aircraft) and March 2000 (boat) by National Environmental Research Institute, Denmark and the Greenland Institute of Natural Resources. Dotted lines are district borders. Danish names of towns are: Ilulissat = Jakobshavn, Sisimiut = Holsteinsborg, Maniitsoq = Sukkertoppen, Nuuk = Godthåb, Paamiut = Frederikshåb, Qaqortoq = Julianehåb, Tasiilaq = Ammassalik.

sites (J. Rosing, personal communication). Farther north in East Greenland a few birds have been observed or collected in the Scoresbysund District at 70°30' N and 68° N, but only in marine habitats (Pedersen 1930; Andersen 1981*).

The breeding habitats are mainly found at elevations below 150 m above sea level. However, some records from higher elevations inland are reported from the Nuuk District (Table 1). At three sites females with chicks were observed at sea near river outlets (Bennike 1990; A. Mosbech, personal communication; F. Wille, personal communication).

The winter observations and 35 specimens collected between November and March were all from between Maniitsoq and Nanortalik in West Greenland (Table 2; Figure 1). Most observations were from Nuuk and Paamiut Districts, and the southern part of Paamiut District near Arsuk seems to be a preferred area in winter (Helms 1893; H. Korning, personal communication; B. Knudsen, personal communication).

The earliest birds from inland fjord habitats away from the winter sites were collected on 3 May at Arsuk and on 20 May in Nanortalik District. Harlequin Ducks have been recorded in freshwater habitats on 14 May (Knudsen 1935) in extreme South Greenland and on 6 June on Disko Island in central West Greenland (Kampp and Kristensen 1980*). Near Arsuk many paired birds were observed at a river outlet in a fjord on 10 June and 18 June (K. Kampp, personal communication). Spring migration has only been reported twice: A pair flew into the fjord at Nuuk on 24 May 1999 (M. Kviesgaard, personal communication) and eight birds (two males, six females/immatures) flew north at Ilulissat town on 17 June 1999 (E. Mogensen, personal communication).

Discussion

Breeding birds

Most of the breeding and probable breeding records are from Paamiut, Nuuk, and southern Maniitsoq Districts. It is reasonable to assume that this reflects higher breeding density in these districts, although the data could be biased by the fact that the human populations are larger there, particularly in Nuuk (the capital of Greenland). The apparently very low breeding density in the southern districts of Qaqortoq, Narsaq and Nanortalik seems to be real, as this region also has a relatively large human population. From central Maniitsoq and northwards there are very few records, and large areas seem to be devoid of Harlequin Ducks. For example, none were observed in suitable areas in interior parts of Kangaatsiaq District despite extensive ornithological fieldwork there (Fox and Stroud 1981*; Fox et al. 1991*; C. Glahder, personal communication). Large parts of Uummannaq District also seem unsuited to Harlequin Ducks due to the extreme alpine topography. The breeding population in East Greenland is apparently very small and restricted to a few sites. However, human activity is also very limited in this part of Greenland, and breeding pairs could be widely dispersed, as indicated by the observation at Skjoldungen. The few records in Scoresbysund District could be of breeding birds from interior parts of the fjord system or, alternatively, stragglers from Iceland.

The Harlequin Duck's total breeding range in West Greenland covers about 50 000 km^2 (below 300 m asl), where rivers and streams are numerous. Only small parts of these rivers seem to be utilised by Harlequin Ducks. Many rivers are probably avoided due to the turbid melt-water draining from the inland ice or local glaciers, but others with clear water also fail to attract

TABLE 2. Summary of 155 study skins of full grown Harlequin Ducks collected in Greenland and kept in Zoological Museum of Copenhagen. (ads = adults; imms = immatures; juvs = juveniles; n.a. = not aged).

Month	Males			Females				Total	Total with location	Districts
	ads	imms	juvs [a]	ads	imms	juvs [a]	n.a			
January	6	1	-	0	0	-	0	7	3	Man, Nuuk
February	8	1	-	1	0	-	1	11	1	Nuuk, Pam, Nan
March	6	0	-	1	0	-	0	7	0	Nuuk, Qaq
April	9	0	-	0	0	-	0	9	1	Nuuk, Pam
May [b]	7	0	-	2	1	-	3	13	6	Man, Nuuk, Pam, Qaq
June [b]	19	8	-	2	5	-	0	34	18	Sis, Man, Nuuk, Qaq, Pam, Tas, Sco
July	7	2	-	3	6	-	0	18	12	Dis, Man, Nuuk, Tas
August	14	1	1	0	0	-	3	19	15	Dis, Sis, Man, Nuuk, Tas
September	11	0	0	3	1	3	3	21	15	Ilu, Sis, Man, Nuuk, Pam, Tas
October	2	0	0	0	0	1	3	6	2	Man, Nuuk, Pam, Qaq
November	3	0	2	1	0	1	0	7	1	Man, Nuuk
December	2	0	0	0	0	1	0	3	0	Nuuk, Nan
Total	94	13	3	13	13	6	13	155	74	

[a] only first calendar year birds; after 31 Dec. listed as immatures, [b] includes a pair from a breeding habitat. Districts: Ilu = Ilulissat, Dis = Disko Island, Sis = Sisimiut, Man = Maniitsoq, Nuu = Nuuk, Pam = Paamiut, Qaq = Qaqortoq (incl. Narsaq), Nan = Nanortalik, Tas = Tasiilaq, Sco = Scoresbysund

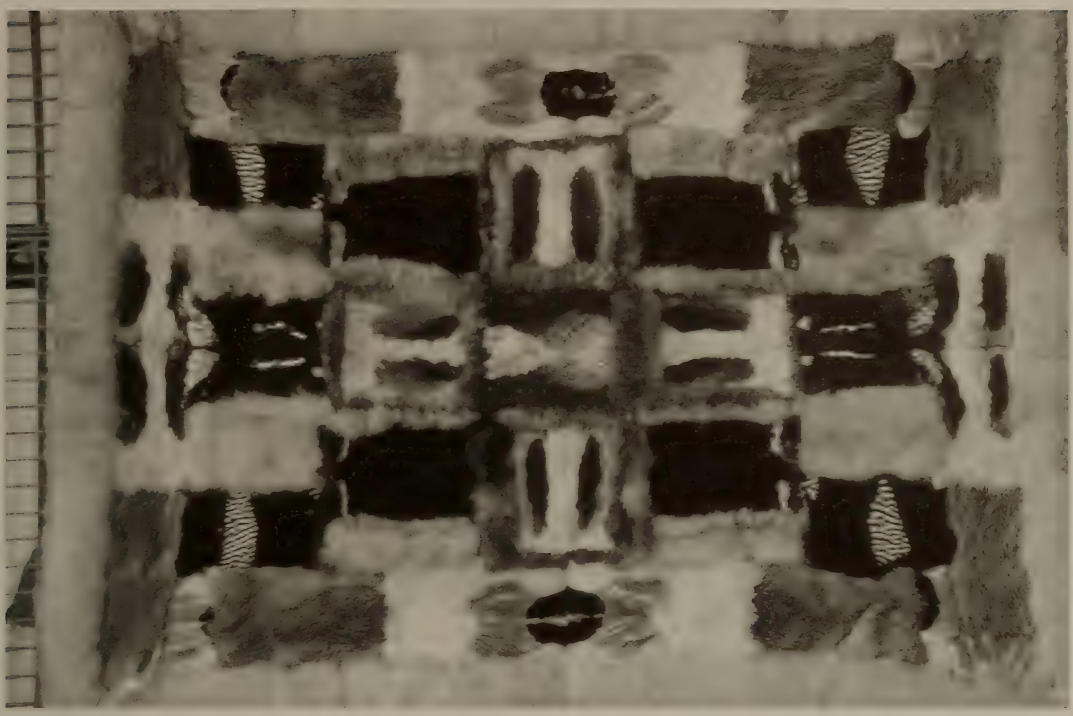


FIGURE 2. Bird skin rug from Qassimiut in Qaqortoq District. The border is made from Common Eider skins, where feathers are removed and down layer is intact. The pattern is made up from head and/or neck skins of Common Eider (both male and female), Common Loon, Mallard (male), Long-tailed Duck (male) and Harlequin Duck (male).

Harlequin Ducks. In Iceland and Canada food abundance seems to limit the breeding populations (Bengtson and Ulfstrand 1971; Bengtson 1972; Rodway 1998), and it is possible that production in many Greenland rivers is insufficient, perhaps related to the low water temperatures. This could also explain why most breeding records are from inland sites where the climate is more continental, with more sunny days and higher temperatures than in areas closer to Davis Strait. Another factor that helps explain the paucity of breeding records is the fact that people in Greenland travel mostly by boat along the coasts, and rarely venture far inland except when hunting Caribou, *Rangifer tarandus,* in August and September. The size of the breeding population of Harlequin Ducks in Greenland is undoubtedly small, and an educated guess may be a few thousand pairs.

Wintering birds

Winter records (Figure 1) are all from the region where open water is reliably available in winter. In this region the probability of sea ice being present in February and March, when ice cover is most extensive, is less than 50%, and when the ice eventually does occur the coverage is usually low (Valeur et al. 1997*). The wintering birds consist of the local breeding population (although no definite proof is available) and of the eastern Canadian breeding population. The latter were confirmed by a few signals in December to April from three birds equipped with satellite transmitters in 1998 (Brodeur et al. 2002). It is uncertain, however, how many Canadian males actually winter in West Greenland. In 2001 males were tracked by satellite from winter quarters in Maine to moulting sites in Greenland (G. Mittelhauser and M. Robert, personal communication). Thus, at least some males may leave Greenland after moulting. Females and juveniles usually join the males at non-breeding sites (Robertson and Goudie 1999), where courtship behaviour and pair formation take place in the autumn (Gowans et al. 1997; Robertson et al. 1997). These activities have not been confirmed for Canadian males in West Greenland. An observation of four females or juveniles migrating 40 km off the coast of Paamiut on 12 October 1993 (Boertmann and Mosbech 2001*) could have been Canadian birds on their way to Greenland.

The number of wintering Harlequin Ducks in Greenland is unknown, but an estimated 5000-10000 males moult in West Greenland (Boertmann and Mosbech 2002). The low numbers estimated to winter in eastern Canada and the USA imply that only a portion of the moulting Canadian males return there for the winter. If females and juveniles join the remaining males

in Greenland, the winter population there may be substantially augmented. Even without the Canadian females and juveniles, the coasts of southern West Greenland are, at least during the moulting season, extremely important to the survival of the breeding populations of Harlequin Ducks in both eastern Canada and Greenland.

Breeding phenology

The few observations indicate that Greenland Harlequin Ducks arrive at or near the breeding habitats during May and June, and generally later at northern than at southern sites.

Early clutches seem to be initiated around 1 June and the majority apparently later in June, assuming a maximum egg-laying period of 10 days, an incubation period of 28 days and a fledging period of 6 weeks (Bengtson 1972; Cramp and Simmons 1977). Observations of chicks in mid- and late September show that some clutches are initiated as late as mid-July (Table 1). Spring observations of migrating birds and birds staging at Arsuk suggest that mid- or late June is the peak initiation period. However, clutch initiation probably varies with both latitude and elevation of the breeding location and also among years due to climatic fluctuations. Compared to other sites, timing in Greenland seems essentially similar to that reported from Iceland in the 1960s (Bengtson 1972), and somewhat earlier than reported from northern Labrador in 1996 (Rodway 1998).

Local knowledge and use

The Greenlandic name of the Harlequin Duck, "Toornaviarsuk," derives from "Toornaq" which is an assisting spirit in Greenlandic mythology. "Toornaviarsuk" may then be translated as "a funny little spirit". It gives an impression of a mysterious and intangible creature (Salomonsen 1974), encountered only in waters that are difficult to navigate or at remote inland sites.

Many sites in Greenland are named after birds or mammals. Only one site named after the Harlequin Duck has been located during this study. A small island near Qeqertarsuatsiaq is called Toornaviarsuit, the plural form of "Toornaviarsuk". This site is exposed to the open sea and is typical moulting and wintering habitat for Harlequin Ducks. On 21 July 1999 a flock of 20 moulting Harlequin Ducks were observed at this island during an aerial survey (Boertmann and Mosbech 2002).

In a few settlements in West Greenland traditional birdskin rugs still are manufactured. These are mainly made from eiders, but ornamental skin parts from other species such as Common Loon (*Gavia immer*), Mallard (*Anas platyrhynchos*) and Long-tailed Duck (*Clangula hyemalis*) often are included. In rugs from the settlement Qassimiut in Qaqortoq District head and neck skins of male Harlequin Ducks (in alternate plumage) sometimes appear (Figure 2), despite the fact that the species is fully protected in Greenland.

Conservation and Threats

The Harlequin Duck was given full protection in Greenland in 1963, because the breeding population was considered too small to withstand increasing international demand for eggs and birds to stock aviculture holdings and zoological gardens (Salomonsen 1967). Nevertheless, Harlequin Ducks are shot occasionally, either for consumption or to obtain the skin (see above). Harlequin Ducks are particularly vulnerable to increased adult mortality (Goudie et al. 1994), but the number killed in Greenland is very low and probably insignificant in terms of population impacts.

The construction of a hydropower plant south of Nuuk in 1993 dried out a river where several pairs of Harlequin Ducks had bred (Aastrup and Nygaard 1986*). Other hydropower plants are in the planning stages, some of them at rivers inhabited by Harlequin Ducks. These are among the few specific examples in Greenland where human activities have destroyed, or threaten to destroy, bird habitat.

Marine oil spills are a serious threat to Harlequin Ducks (Lanctot et al. 1999; Esler et al. 2000), and in West Greenland local breeding populations and the eastern Canadian breeding population are at risk. Half of the 200 000 tons of fuel oil shipped to Greenland annually is unloaded to a tank site at Færingehavn at 63°45' N (J. Rosenberg, personal communication). This site is adjacent to very important Harlequin Duck moulting and wintering sites, holding up to 1000 males in July (Boertmann and Mosbech 2002). Offshore oil exploration drilling was carried out about 150 km west of Nuuk in 2000, and more such drilling is expected in the future. Oil spill trajectory modelling from the 2000 drill site predicted that oil would hit the Greenland coast somewhere between 62° and 68° N (Mosbech et al. 1996*). The southern part of this coastline (62° – 64° N) held about 70% (2488 birds) of the moulting male Harlequin Ducks recorded in July 1999 (Boertmann and Mosbech 2002).

The risk of by-catch of Harlequin Ducks in gillnets is probably low, as fisheries for Lumpsucker, *Cyclopterus lumpus,* and Arctic Char, *Salvelinus alpinus,* take place mainly in fjords and sheltered bays away from the exposed Harlequin Duck habitats. However, the bycatch issue should be examined more closely.

Very few Harlequin Duck habitats are protected in Greenland. Two of the eleven sites in Greenland on the Ramsar List of Wetlands of International Importance (Ramsar Convention on Wetlands) include moulting and wintering sites for Harlequin Ducks, and an area protected mainly due to archaeological and botanical interests also includes a river with breeding Harlequin Ducks.

Future research

The general knowledge on ecology, distribution and abundance of the Harlequin Duck in Greenland is very limited. One of the most urgent research needs is to estimate the size of the breeding population. Once

such an estimate is available, it should be possible to determine the approximate size of the Canadian contingent among the moulting males in West Greenland. In turn, such a determination would contribute to efforts to estimate the eastern Canadian breeding population.

Acknowledgments

Anders Mosbech, Lars Vilhelmsen, Peter Aastrup, Birger Knudsen, Preben Grossmann, Kaj Kampp, Knud Falk, Jens Rosing, Frank Wille, Jørn Rosenberg, Bjarne Persson, Ole Vognsen and Egon Mogensen provided local knowledge and unpublished observations. The Zoological Museum in Copenhagen gave access to its collection and files, and the author was assisted there by Jan Bolding and Kaj Kampp. Kristjana Motzfeldt allowed me to study her birdskin rug, Helene Brochmann translated Greenlandic words and Jean-Pierre Savard, Ian Goudie and Michael Rodway commented on and improved earlier drafts of the manuscript. A. J. Erskine improved the final manuscript and Randall Reeves improved the English. My sincere thanks to all.

Documents Cited (marked * in the text)

Aastrup, P., and **K. Nygaard.** 1986. Miljømæssig vurdering af vandkraftprojekt Kangerluarsunnguaq/Buksefjord Nuuk/Godthåb. Grønlands Fiskeri- og Miljøundersøgelser. Technical Report.

Andersen, J. 1981. Kaptajn Ejnar Mikkelsens Mindeekspedition 1980. Scoresbysund - Angmagssalik. Field Report.

Boertmann, D., and **A. Mosbech.** 2001. Offshore seabird distributions during summer and autumn at West Greenland. Ship based surveys 1977 and 1992-2000. National Environmental Research Institute, Denmark. Technical Report number 370.

Brodeur, S., M. Robert, P. Laporte, G. Fitzgerald, A. Bourget, S. Marchand, P. Lamothe, S. Gilliland, and **J-P. L. Savard**. 1999b. Suivi satellitaire des déplacements de Canards arlequins (*Histrionicus histrionicus*) nichant dans l'est de l'Amérique du Nord (1996-1998). Technical Report Series Number 332. Canadian Wildlife Service, Quebec Region.

Fox, A. D., and **D. A. Stroud.** *Editors*. 1981. Report of the 1979 Greenland White-fronted Goose Study Expedition of Eqalungmiut Nunat, West Greenland. GWGS Aberystwyth.

Fox, A. D., **J. Feilberg**, **J. Salvig**, and **H. Ettrup.** 1991. Biologisk registrering på Naternaq (Lersletten), Vestgrønland juli 1991. Field report.

Kampp, K., and **R. M. Kristensen.** 1980. Fugle på Disko - Vestgrønland. Unpublished Report.

Mittelhauser, G. H. 2000. The winter ecology of Harlequin Ducks in coastal Maine. Technical report NPS/BSO-RNR/NRTR/00-16. Department of the Interior, National Park Service, Boston, Massachusetts.

Mosbech, A., R. Dietz, D. Boertmann, and **P. Johansen.** 1996. Oil exploration in the Fylla Area. National Environmental Research Institute, Denmark. Technical Report 156.

Valeur, H. H., C. Hansen, K. Q. Hansen, L. Rasmussen, and **N. Thingvad.** 1997. Physical environment of eastern Davis Strait and northeastern Labrador Sea. Danish Meteorological Institute Technical Report 97-9 (2 volumes).

Literature Cited

Bengtson, S-A. 1972. Breeding ecology of the Harlequin Duck *Histrionicus histrionicus* (L.) in Iceland. Ornis Scandinavica 3: 1-19.

Bengtson, S-A., and **S. Ulfstrand.** 1971. Food resources and breeding frequency of the harlequin duck *Histrionicus histrionicus* in Iceland. Oikos 22: 235-239.

Bennike, O. 1990. Observations of geese and other birds in West Greenland, 1989 and 1990. Dansk Ornithologisk Forenings Tidsskrift 84: 145-150.

Bertelsen, A. 1921. Fuglene i Umánaq distrikt. Meddelelser om Grønland 62 (2): 139-214.

Boertmann, D. 1979. Ornithological observations in West Greenland, 1972-77. Dansk Ornithologisk Forenings Tidsskrift 73: 171-176. (Danish, with English summary).

Boertmann, D. 1994. An annotated checklist to the birds of Greenland. Meddelelser om Grønland, Bioscience 38: 1-63.

Boertmann, D., and **A. Mosbech.** 2002. Moulting Harlequin Ducks in Greenland. Waterbirds 25: 326-332.

Brodeur, S., J-P. L. Savard, M. Robert, and **G. Fitzgerald.** 1999a. Satellite telemetry confirms the existence of two separate populations of Harlequin ducks in eastern North America. Wetlands International Seaduck Specialists Group Bulletin 8: 34.

Brodeur, S., J-P. L. Savard, M. Robert, P. Laporte, P. Lamonthe, R. D. Titman, S. Marchand, S. Gilliland, and **G. Fitzgerald.** 2002. Harlequin Duck *Histrionicus histrionicus* population structure in eastern Nearctic. Journal of Avian Biology 33: 127–137.

Cramp, S., and **K. E. L. Simmons.** *Editors*. 1977. The Birds of the Western Palearctic, Volume 1. Oxford University Press, Oxford.

Esler, D., J. A. Schmutz, R. C. Jarnis, and **D. M. Mulcahy.** 2000. Winter survival of adult female harlequin ducks in relation to history of contamination by the *Exxon Valdez* oil spill. Journal of Wildlife Management 64: 839-847.

Goudie, R. I. 1991. The status of the Harlequin Duck (*Histrionicus histrionicus*) in eastern North America. Report to Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, Ontario.

Goudie, R. I., S. Brault, B. Conant, A. V. Kondratyev, M. R. Petersen, and **K. Vermeer.** 1994. The status of seaducks in the North Pacific rim: towards their conservation and management. Transactions of the North American Wildlife and Natural Resources Conference 59: 27-49.

Gowans, B., G. J. Robertson, and **F. Cooke.** 1997. Behaviour and chronology of pair formation by Harlequin Ducks *Histrionicus histrionicus*. Wildfowl 48: 135-146.

Helms, O. 1893. Ornithologiske Iagttagelser fra Arsukfjorden, Sydgrønland. Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjøbenhavn for Aaret 1892: 221-252.

Helms, O. 1926. The birds of Angmagssalik. Meddelelser om Grønland 58 (4): 205-274.

Knudsen, K. 1935. Noter om Lindenowfjords fuglefauna. Dansk Ornithologisk Forenings Tidsskrift 29: 37-41.

Lanctot, R., B. Goatche, K. Scribner, S. Talbot, B. Pierson, D. Esler, and **D. Zwiefelhofer.** 1999. Harlequin Duck recovery from the *Exxon Valdez* oil spill: A population genetics perspective. Auk 116: 781-791.

Oldenow, K. 1933. Fugleliv i Grønland. Det grønlandske Selskabs Aarsskrift 1932-33: 17-224.

Pedersen, A. 1930. Forgesetzte Beitrage zur kenntnis der Säugetiere- und Vogelfauna der Ostküste Grönlands. Meddelelser om Grønland 77 (5): 343-507.

Petersen, A. 1998. Ìslenskir fuglar. Vega-Helgafell, Reykjavík.

Petersen, A. 2000. Válisti 2. Fuglar. Náttúrufræðistofnun Íslands, Reykjavik.

Robertson, G. J., F. Cooke, R. I. Goudie, and **W. S. Boyd.** 1997. The timing of arrival and moult chronology of Harlequin Ducks *Histrionicus histrionicus*. Wildfowl 48: 147-155.

Robertson, G. J., and **R. I. Goudie**. 1999. Harlequin Duck. *In* The Birds of North America Number 466. *Edited by* A. Poole and F. Gill. American Ornithologists Union.

Rodway, M. S. 1998. Activity patterns, diet, and feeding efficiency of Harlequin Ducks breeding in northern Labrador. Canadian Journal of Zoology 76: 902-909.

Salomonsen, F. 1950. Grønlands Fugle/The Birds of Greenland. Munksgaard, København.

Salomonsen, F. 1967. Fuglene på Grønland. Rhodos, København.

Salomonsen, F. 1974. Fuglene i menneskenes land/Tingmissat kalâtdlit nunane. 1. Det Grønlandske Forlag, Godthåb.

Salomonsen, F. 1979. Thirteenth preliminary list of recoveries abroad of birds ringed in Greenland. Dansk Ornithologisk Forenings Tidsskrift 73: 191-206.

Salomonsen, F. 1981. Fugle. Pages 161-360 *in* Grønlands Fauna. *Edited by* F. Salomonsen. Gyldendal, København.

Secher, K., J. Böcher, B. Grønnow, S. Holt, H. C. Petersen, and **H. Thing.** 1987. Arnangarnup Qoorua. Paradisdal i tusinder af år. Pilersuiffik, Nuuk.

Vickery, P. D. 1988. Distribution and population status of Harlequin Ducks (*Histrionicus histrionicus*) wintering in Eastern North America. Wilson Bulletin 100: 119-126.

Received 11 April 2002
Accepted 30 October 2003

Effects of Season of Burning on the Microenvironment of Fescue Prairie in Central Saskatchewan

O. W. Archibold[1], E. A. Ripley[2], and L. Delanoy[3]

[1]Department of Geography, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5A5 Canada
[2]Department of Plant Sciences, University of Saskatchewan, Saskatoon Saskatchewan S7N 5A8 Canada
[3]Meewasin Valley Authority, 403 3rd Avenue South, Saskatoon, Saskatchewan S7K 3G5 Canada

Archibold, O. W., E. A. Ripley, and L. Delanoy. 2003. Effects of season of burning on the microenvironment of fescue prairie in central Saskatchewan. Canadian Field-Naturalist 117(2): 257-266.

The microenvironmental effects of spring, summer and autumn burns were investigated for a small area of fescue prairie in Saskatchewan over two growing seasons. Maximum fire temperature in all burns exceeded 300°C at a height of 5-10 cm in the canopy. At a depth of 1 cm in the soil, temperature increased to 40°C during the summer burn, but was unaffected by burns at other seasons. Spring-burned grasses recovered to the same height as the unburned control plot by the end of the first summer. Grass height was similar in all plots by the end of the second growing season, but aboveground biomass in all burned plots was about half that of the control. Graminoid leaf area index at the end of the second growing season ranged from 0.65 in the control plot to 0.27 in the autumn burn. Surface albedos dropped to about 0.03 immediately after burning and took about 3 months to return to the pre-burn values near 0.20. By mid-June of the second year, albedos were similar in all plots. Soil temperatures at 50 cm depth in the burned plots were higher than in the control during the first summer and lower during the winter. The greatest winter snowpack (73 mm water equivalent) accumulated in the control, compared to 48, 35 and 25 mm in the spring, summer and autumn burned plots, respectively. In the first growing season the greatest demand for water occurred in the spring plot followed by the summer, control and autumn plots. In the second season water demand did not differ significantly among plots, reflecting the similarities in plant cover. The microenvironmental effects of a single burning episode in fescue prairie disappear rather quickly, so that there is little long-term impact on the vegetation.

Key Words: Plains Rough Fescue, *Festuca altaica* subspecies *hallii*, albedo, fire, microclimate, snow cover, soil temperature, soil moisture, Saskatchewan.

Fire is an important natural element in prairie environments of North America. Originally there were few firebreaks to stop its progress and native species are well adapted to periodic burning (Daubenmire 1968; Vogl 1974). Although natural fires have become less common, prescribed burning is used to improve forage quality through recycling nutrients, to decrease litter accumulation and to eliminate weeds and woody vegetation. Because water loss typically increases after burning (Anderson 1965), prescribed burns are not recommended in the northern Great Plains during periods of drought (Engle and Bultsma 1984; White and Currie 1983). There is an extensive literature on the ecological effects of grassland fires and species response to fire frequency, fire intensity and time of burning (see for example: Anderson et al. 1970; Ewing and Engle 1988; Redmann et al. 1993; Romo et al. 1993). The extent and frequency of burning has declined with the spread of agriculture across the Canadian prairies (Raby 1966). This has led to the invasion of woody species and the build-up of large amounts of standing dead vegetation and thatch, creating a fire hazard to adjacent agricultural land. To counteract these trends, prescribed burning was introduced in the northern Great Plains and many studies have been undertaken to establish the optimum frequency and timing of burning (Romo et al. 1993; Steuter 1987; White and Currie 1983; Wright and Bailey 1980; Vogl 1974).

Grassland fires subject aboveground plant parts to temperatures as high as 600°C (Bailey and Anderson 1980; Archibold et al. 1998), killing most plant tissue and exposing the soil surface. Species growing actively when the area is burned are more susceptible to injury than dormant species or those just initiating growth (Anderson et al. 1970). The fire front passes quickly across the fine fuel so there is little heat penetration into the soil; temperatures immediately below the surface rarely exceed 50°C (Tester 1965). Soils exposed by early season burning warm more rapidly than in unburned areas and growth typically begins earlier in the spring. This can increase water demand. Conversely, late season fires allow the exposed soil to cool more rapidly in autumn (Peet et al. 1975). However, few studies have measured how burning affects the microenvironment of temperate grasslands. When a vegetation canopy is removed by fire, the surface energy balance is changed (Bremer and Ham 1999) which leads to modifications in the aboveground and belowground microclimates (Ewing and Engle 1988; Old 1969). There are several reasons for this: aerodynamic changes occur as the wind penetrates closer to the surface, transporting heat and water vapour more rapidly than before; the surface albedo diminishes due to the exposure of soil (Bowers and Hanks 1965) and the deposition of burnt organic material; and the removal of most transpiring leaves limits moisture loss to direct

soil evaporation. The immediate result is that more solar energy is absorbed at the soil surface, increasing soil evaporation and daytime heat flow into the soil and atmosphere. The lack of an insulating cover of vegetation allows heat to be radiated away more rapidly at night. The effects of burning in one year therefore can affect plant growth in subsequent years, especially in regions where precipitation is quite variable.

The present study compares the microenvironments of unburned fescue prairie in plots burned in spring, summer and autumn of 1998. The effect of time of burn on vegetation regrowth was monitored over two growing seasons together with the impact of seasonal fires on the microenvironment of the burned plots. This study provides an assessment of the effects of season of burning on the prairie microenvironment with a view to predicting differences in vegetation growth and water use. This information will assist explaining time-of-burning impacts on species growth and composition and provide a better understanding of the use of fire as a management tool in fescue prairie grassland. The paucity of previous studies in this area may reflect the difficulties involved in setting up such an experiment, which also constrained the present study to a single plot for each treatment.

Study area

Prescribed burning was carried out at Kernen Prairie, a remnant fescue prairie stand near Saskatoon, Saskatchewan (52°11′N, 106°42′W), during the 1998 growing season; the selected area had last been burned in May 1991. As described by Pylypec (1986) the dominant grass at the site is Plains Rough Fescue (*Festuca altaica* subsp. *hallii)* which grows in association with Kentucky Bluegrass (*Poa pratensis*) and sedges (*Carex heliophila, C. obtusata*). Several forbs including asters (*Aster falcatus, A. laevis*), Northern Bedstraw (*Galium boreale*), Three-flowered Avens (*Geum triflorum*) and Prairie Sage (*Artemisia ludoviciana*) are also present together with the low growing shrub Western Snowberry (*Symphoricarpos occidentalis*) and roses (*Rosa* spp.) (Pylypec 1986). Soils in this area are fine-textured chernozems derived from glacio-lacustrine clays; they have a surface dry bulk density of 1.33 g cm^{-3}.

The region experiences a continental climate with mean monthly temperatures ranging from –18°C in January to 19°C in July; average annual precipitation is 360 mm, of which about 30% falls as snow (Atmospheric Environment Service 1993). During the growing season mean monthly temperatures increase from 11°C in May to 19°C in July and drop to 11°C by September. In 1998 temperatures averaged 2-3°C above normal in May, 1-2°C below normal in June and near normal in July, with warmer than normal conditions prevailing until the end of the year (Atmospheric Environment Service 1998, 1999). In 1999 temperatures averaged 1-2°C below normal except for near normal conditions in August. Monthly precipitation normally averages about 20 mm during the winter months, rising in the spring to a peak of 60 mm in June and July, and returning to winter values by October. In 1998 precipitation was light early in the growing season, then near normal except for a rainy August; the April to September total averaged 5% above normal. In contrast, 1999 was considerably wetter, except for August and September, with 17% above normal precipitation during April to September (Figure 1).

Methods

Four contiguous 10 × 10 m plots were established in April 1998. One was maintained as a control and the remaining plots were burned in the spring (6 May 1998), summer (26 June 1998) and autumn (8 October 1998), respectively. Instruments were installed in all plots to measure reflected solar radiation (Li-Cor LI-200SZ pyranometer), soil temperatures at 2, 10 and 50 cm (Campbell Scientific Model 107 thermistor temperature probe) and soil water content of the 0-30 cm layer (Campbell Scientific CS615 TDR – time domain reflectometry – probe). Unfortunately, animals frequently damaged the instrument cables, so some of the data for the 2 cm soil temperatures, TDR and solar radiation are missing. Incoming solar radiation and precipitation (Campbell Scientific Model TE525 tipping-bucket rain gauge) were measured at a single point in the control plot. The microclimate data were recorded (Campbell Scientific CR10) from 12 May 1998 until 19 October 1999. Snow depth and water equivalent of the snow pack were measured at 30 points in each plot in February 1999, which is usually the month of maximum snow cover in Saskatchewan. Soil water content was measured by neutron probe every 2-4 weeks in each plot to a depth of 100 cm.

Fuel load and moisture content were determined from samples collected at 12 0.25 × 0.50 m quadrats within the prescribed plot prior to each burn. All aboveground vegetation was cut and bagged. The samples were sorted into live and standing dead graminoids, forbs, shrubs and litter, weighed to establish biomass, dried in an oven at 90°C and re-weighed. Additional samples, processed in the same manner, were used to determine changes in live and standing dead biomass and litter within the control and treatment plots during each year of the study.

Fire temperatures were measured during each burn at 1 cm depth in the soil and at heights of 5, 10, 20, 50 and 100 cm above ground. Four replicate chromel-alumel thermocouples were used at each position. The temperatures were recorded every 10 seconds using Campbell CR10 dataloggers. Burning was carried out after establishing a firebreak around the selected plot, and a ring fire was then set to burn towards the temperature probes.

The fescue community is associated with lower topographic positions within Kernen Prairie (Baines 1973) and the sample area was selected because of

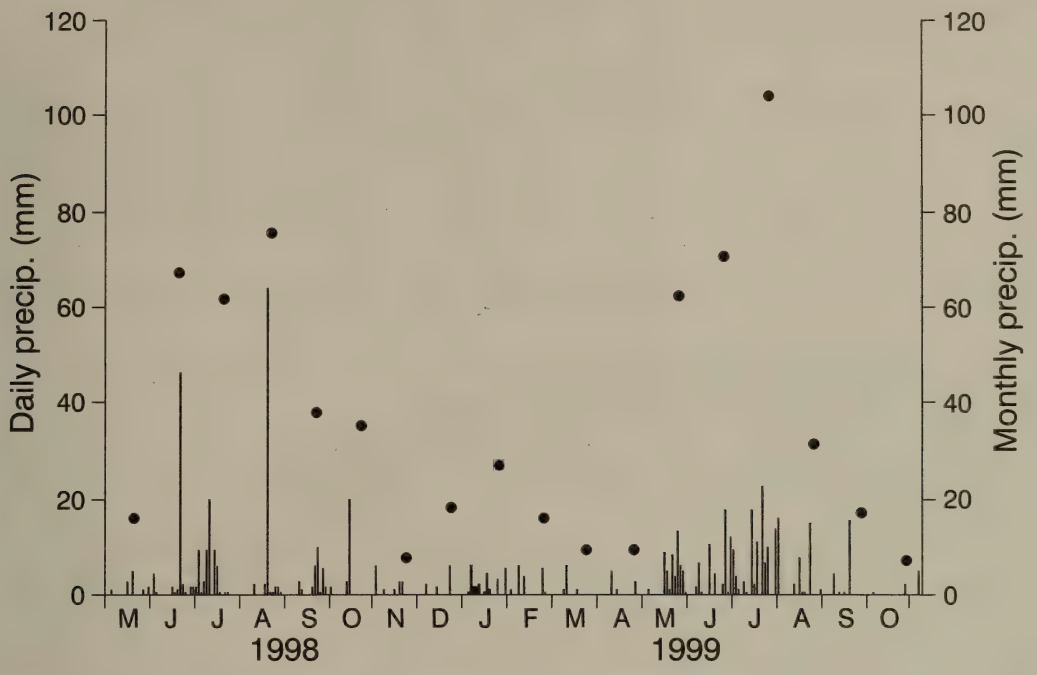


FIGURE 1. Daily (bars) and monthly (dots) precipitation at the study site.

uniformity of the pre-burn plant cover, soil conditions and topography. A vegetation survey of the control and burned plots was carried out at the end of the second growing season. Species composition was measured at each plot using twelve 0.5×0.5 m quadrats set out in three parallel transects. Density (stems m^{-2}) was an appropriate measure for the forbs and shrubs, because of their discrete growth habits and comparatively small populations. Percent cover was used for graminoids because of the difficulty of distinguishing individual plants. Leaf area index (LAI) was determined for graminoids, forbs and shrubs collected from eight 0.25×0.50 m quadrats in each of the treatment plots and control. The samples were processed using a Li-Cor LI-3100 Area Meter.

Results and Discussion

(a) *Fire temperatures* — The average fuel load in the spring was 0.67 kg m^{-2}; this had increased to 0.74 kg m^{-2} by summer and reached 0.75 kg m^{-2} in the autumn (Table 1). These fuel loads are about double those reported by Redmann et al. (1993) and Archibold et al. (1998) in similar stands. Moisture content of the combined live and dead fuel load averaged 12.7% and 14.6% at the time of the spring and summer burns, respectively, but increased to 64.5% prior to the autumn burn. Archibold et al. (1998) previously reported a spring moisture content of 44% for fescue prairie. Air temperature at the time of the spring burn was 10°C, relative humidity was 35% and wind speed was 3.0 m s^{-1}. The mean maximum fire temperature observed during the spring burn was 336°C at a height of 10 cm (Table 2). Fire temperatures declined progressively above this height, dropping to 89°C at 100 cm (Figure 2). The mean maximum fire temperature at 5 cm was 227°C and remained above 50°C, a temperature generally recognized as lethal to plant tissue (Martin et al. 1969), for over 5 min. Soil temperatures at 1 cm showed no measurable increase during the fire. During the summer burn air temperature was 26°C, relative humidity was 50% and wind speed was 4.0 m s^{-1}. The highest mean maximum fire temperature was

TABLE 1. Mean (± SD) fuel loads of live and dead material and fuel moisture levels prior to the spring, summer and autumn burns (n =12).

	Spring	Summer	Autumn
Fuel load (g m^{-2})	670.4 ± 334.4	742.4 ± 215.8	748.8 ± 197.6
Fuel moisture (%)	12.7 ± 1.8	14.6 ± 3.4	64.5 ± 17.3

TABLE 2. Mean maximum fire temperatures (°C) and durations above 50°C during the spring, summer and autumn burns.

	Spring		Summer		Autumn	
	Temperature (°C)	50°C Duration (min)	Temperature (°C)	50°C Duration (min)	Temperature (°C)	50°C Duration (min)
100 cm	89	1.0	156	2.7	151	1.7
50 cm	134	1.2	209	3.5	174	2.0
20 cm	292	2.0	269	5.0	280	2.3
10 cm	336	3.0	290	5.7	316	2.7
5 cm	227	5.2	330	7.2	324	3.3
-1 cm	8	0	44	0	14	0

330°C at 5 cm and remained above 50°C for more than 7 min; corresponding values at 100 cm were 156°C and 2.7 min above 50°C. A combination of greater thatch accumulation and drier soil conditions probably contributed to the high soil temperature recorded during this fire. Air temperature was 20°C, humidity 40% and wind speed 2.5 m s^{-1} during the autumn burn. The highest mean maximum fire temperature was 324°C at 5 cm and dropped to 151°C at 100 cm; the longest duration for temperatures above 50°C was 3.3 minutes at 5 cm. Soil temperatures did not increase during the autumn burn. Fire temperatures in all burns were generally lower than reported by Archibold et al. (1998) for fescue, but are comparable to grassland fires reported by Bailey and Anderson (1980).

(b) *Vegetation* — A total of 20 species of forbs was recorded at the study site at the end of the second growing season (Table 3). White Prairie Aster was the most abundant species with densities ranging from 69 stems m^{-2} in the spring plot to 139 stems m^{-2} in the summer plot. Prairie Sage, Northern Bedstraw and Woolly Yarrow (*Achillea millefolium*) were also found in all plots. Three species, Harebell (*Campanula rotundifolia*), Field Chickweed (*Cerastium arvense*) and Bladder Campion (*Silene cucubalis*) were present only in the control plot. Late Yellow Locoweed (*Oxytropis campestris*) occurred only in the summer plot while Prairie Crocus (*Anemone patens*) and American Vetch (*Vicia americana*) were found only in the autumn plot. The restriction of species to a treatment plot likely reflects its comparative rarity at the site rather than a consequence of the fire. Shrubs, represented by rose and Western Snowberry, were ubiquitous, the latter being most abundant. Grass cover ranged from 12.2% in the summer plot to 25.5% in the control. Nine grass species were recorded; Plains Rough Fescue was the most abundant grass with Kentucky Bluegrass and Western Porcupine Grass (*Stipa spartea* var. *curtiseta*) also important. Three sedge species also contributed to the vegetation cover. The spring plot had a higher density of rose and a lower density of Western Snowberry than the other plots; some herbaceous species, such as White Cinquefoil (*Potentilla arguta*) and Stiff Goldenrod (*Solidago rigida*), also were better represented.

During the first growing season the average height of the grass canopy in the control reached a maximum of 28 cm and increased to 50 cm by the end of the second growing season (Figure 3) with panicles of the grasses extending to an average height of 70 cm. The spring plot greened up quickly but growth was not prolific. By the end of the first season the vegetative canopy reached 26 cm. A small increase occurred in the second season (27 cm) with panicles forming a very diffuse layer at an average height of 59 cm. Toynbee (1987) also has reported a reduction in flowering in fescue following spring burning. Growth was slower in the summer plot and at the end of the second season averaged 20 cm, although panicles projected above the leaf canopy to 73 cm. Air temperature dropped to near freezing soon after the autumn burn and plant growth ceased. This plot went through winter in a blackened state, and in the following growing season the grasses reached a mean height of 22 cm with panicles projecting to 60 cm. The grasses in the control plot were significantly ($P \leq 0.01$) taller than in any treatment plot, and grass height in the spring and autumn burns was also significantly different. Mean shrub height in the control at the end of the second growing season was approximately 40 cm. At this time the shrub cover in the spring burn averaged 25 cm compared to 29 cm in the summer burn and 33 cm in the autumn burn. Shrub height in the control was significantly taller ($P \leq 0.01$) than in all treatment plots; no significant differences were detected between treatments.

Live biomass in the control in May 1998 averaged 0.58 kg m^{-2} (Figure 4). By June this had increased to 0.75 kg m^{-2} and in September reached 0.76 kg m^{-2}. This compares to the September biomass of 0.27 kg m^{-2} in the spring burn. Regrowth in the summer burn commenced quickly after the fire; within one month the biomass totaled 0.09 kg m^{-2} and increased to 0.18 kg m^{-2} by September 1998. The autumn burn did not green up until the following spring. In 1999 plant growth in the control was less prolific than in 1998 and at the end of season biomass was 0.64 g m^{-2}. In all treatments

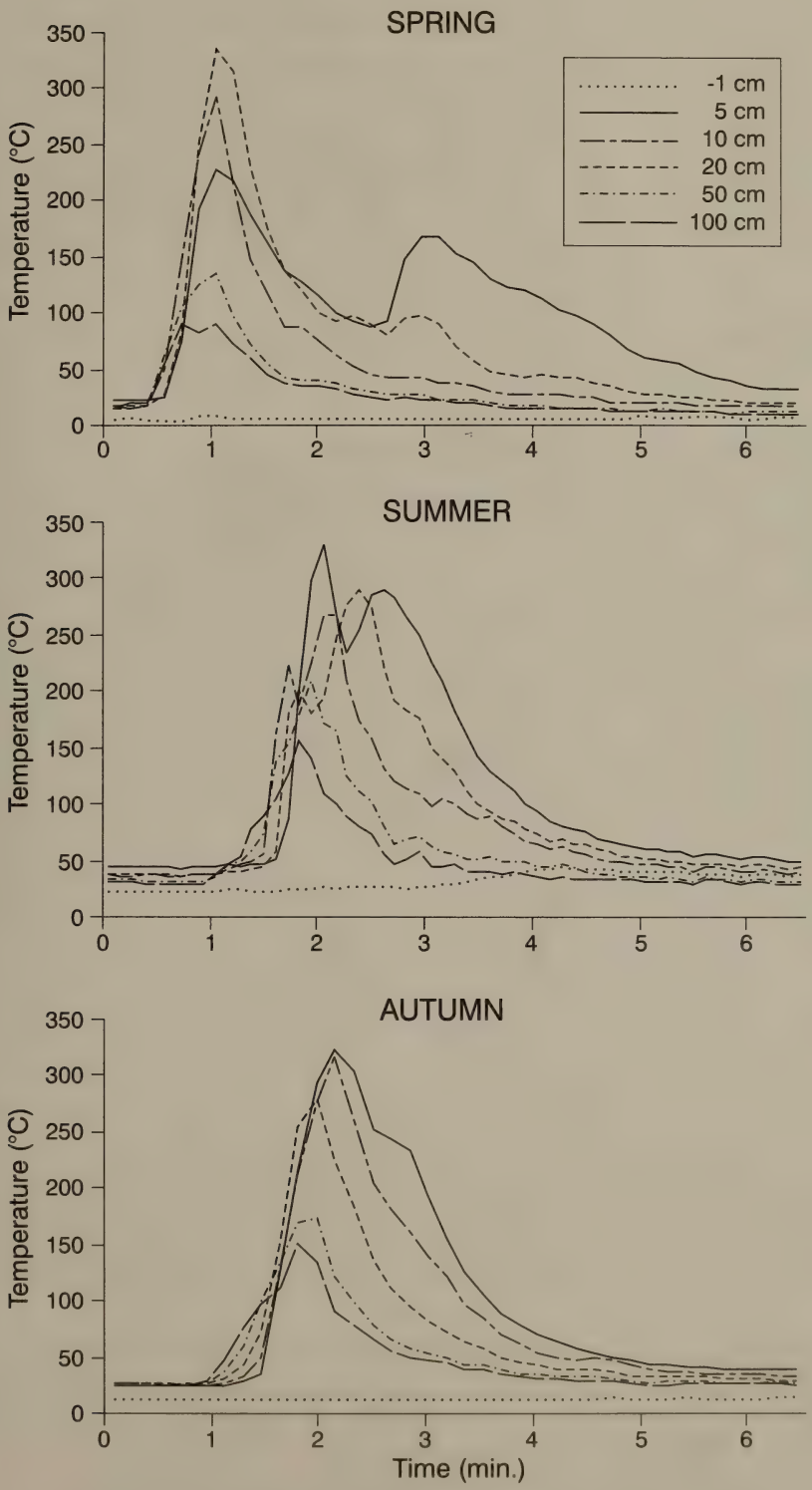


FIGURE 2. Mean fire temperatures at the soil surface and at five heights above ground during the spring, summer and autumn burns.

TABLE 3. Density of forbs and shrubs (stems m^{-2}) and cover of graminoids (%) in the control and burned plots at the end of the second growing season.

	Control	Spring	Summer	Autumn
Forbs				
Achillea millefolium	2.7	8.3	1.7	8.3
Androsace septentrionalis	0.7	5.7	14.0	
Anemone patens				1.3
Artemisia frigida	3.7	2.3	1.7	2.7
Artemisia ludoviciana	23.7	9.7	3.3	20.3
Aster falcatus	91.7	69.3	138.7	99.3
Aster laevis	1.3	7.3	10.3	
Astragalus goniatus		2.3		13.7
Campanula rotundifolia	2.0			
Cerastium arvense	0.7			
Galium boreale	13.0	8.3	5.0	17.0
Geum triflorum	0.7	9.3	11.7	
Oxytropis campestris			14.3	
Phlox hoodii	1.7	1.3	0.7	0.7
Potentilla arguta		4.7	1.7	0.7
Silene cucubalis	0.3			
Solidago missouriensis	0.3	0.3	11.0	
Solidago rigida		6.0	0.3	
Vicia americana	0.3			0.7
Viola adunca	0.0	2.7	2.0	
Shrubs				
Rosa spp.	4.3	17.3	1.0	1.7
Symphoricarpos occidentalis	37.3	28.7	42.3	35.7
Grasses				
Agropyron dasystachum	0.1		0.1	0.1
Agropyron smithii			0.1	0.2
Agropyron subsecundum	1.3	0.5	0.1	0.3
Festuca altaica	11.3	13.2	7.0	8.8
Helictotrichon hookeri				0.1
Koeleria cristata		0.2		0.1
Poa pratensis	6.8	0.2	1.3	5.4
Stipa spartea	5.6	4.9	3.0	2.2
Stipa viridula	0.5	0.2	0.7	1.5
Sedges				
Carex eleocharis	0.4	0.1	0.3	0.7
Carex obtusata	1.0	1.0		
Carex heliophila	1.4	2.6	3.2	3.7

plant biomass in 1999 exceeded that of the previous year; a similar pattern of was noted by Redmann et al. (1993) with full recovery usually occurring in the third post-fire season. (Clarke et al. 1943; Dix 1960). The contribution of graminoids to end of season biomass was highest in the control plot and decreased progressively in the spring, summer and autumn burns (Table 4). Significant differences in grass biomass were noted between the control and the summer and autumn plots ($P \leq 0.05$, df = 12). In contrast, forb biomass was low-

TABLE 4. Mean biomass (g $m^{-2} \pm$ SD) for grasses, forbs and shrubs in the spring, summer and autumn burns at the end of the second growing season.

	Control	Spring	Summer	Autumn
Grasses	$0.40 \pm 0.09^{a*}$	0.26 ± 0.03^{ab}	0.17 ± 0.03^{b}	0.17 ± 0.05^{b}
Forbs	0.06 ± 0.01^{a}	0.14 ± 0.03^{a}	0.11 ± 0.02^{a}	0.08 ± 0.04^{a}
Shrubs	0.18 ± 0.04^{a}	0.03 ± 0.01^{ab}	0.09 ± 0.02^{ab}	0.31 ± 0.07^{b}

*Values in the same row with the same letter are not significantly different ($P \leq 0.05$)

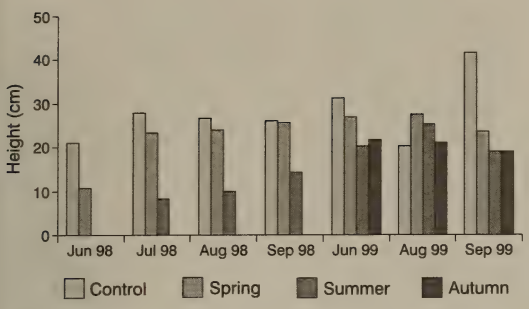


FIGURE 3. Mean vegetation height in the control and spring, summer and autumn burns at selected times during the 1998 and 1999 growing seasons.

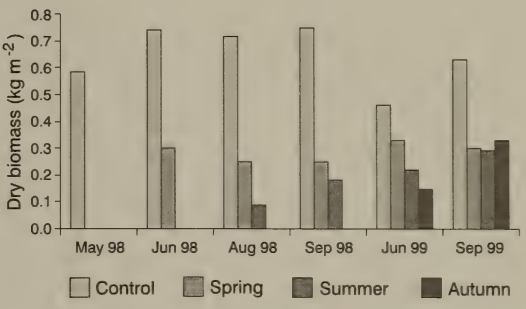


FIGURE 4. Total biomass in the control and spring, summer and autumn burns at selected times during the 1998 and 1999 growing seasons.

est in the control plot and highest in the spring burn, although interplot differences were not significant. Shrub biomass was greatest in the autumn burn with significant differences in biomass noted between the autumn plot and the spring and summer plots. The thatch layer in the control plot was approximately 10 cm deep at the end of the second growing season, but no appreciable depth of litter had accumulated in any of the burned plots. Litter biomass in the control plot was 0.11 kg m^{-2} compared to 0.01 kg m^{-2} in the spring; litter was negligible in the summer and autumn plots. Litter accumulates slowly in burned prairie (Dix 1960) and the paucity of litter is considered to be one of the longest lasting impacts of fire (Redmann et al. 1993).

LAI for graminoids was 0.64 in the control which was significantly higher than the LAI in the summer and autumn plots (Table 5). Forb LAI declined with lateness of burn, although all treatments exceeded the value for the control. Conversely, for shrubs LAI increased with lateness of the burn and ranged from 0.04 in the spring plot to 0.50 in the autumn plot; significant differences were noted between the autumn plot and the spring and summer plots.

(c) *Microclimate* — Surface albedos, calculated as the ratio of daily totals of reflected and incoming solar radiation, averaged approximately 20% during the snow-free period (Figure 5). All three burns dropped the albedo to about 3%, which in the spring and summer plots took about 2 months to recover to pre-burn values. This decrease in albedo is greater than reported in other studies. For example, Knapp (1984) reported a drop from 18% to 10% ten days following burning in the tallgrass prairie of Kansas. The change in albedo caused by the autumn burn was obscured by a heavy snowfall a few days later; after the snow melted, the albedo was about 5% and remained at this value until the arrival of the permanent winter snowpack at the beginning of December. The winter albedo reached about 90% in early January when most of the vegetation was covered with snow. This dropped as the snowpack aged and was about 70% just prior to snowmelt in late February. By mid-May 1999 values ranged from 12% for the autumn burn to 15% for the summer burn and 18% for the spring burn and control. By mid-June the albedos of all plots were similar.

In the first growing season the maximum 2 cm soil temperature in the control was 23°C compared to 31°C in the summer plot shortly after it was burned. The 2 cm soil temperature in the autumn plot was unaffected because the surface was covered with snow following the fire, but over winter dropped to -19°C compared to -16°C in the summer plot and -10°C in the control. In the second growing season the surface soils in the summer and autumn plots warmed faster than the control. By mid-summer the maximum 2 cm temperatures recorded in the treatment plots were all similar at 26-27°C compared to 21°C in the control plot.

Soil temperatures at 10 cm in the spring and summer plots increased in the months following burning (Figure 6) and remained about 2°C higher than the control through the summer. By October the 10 cm soil temperatures in all plots were similar, but by mid winter the burned plots were approximately 2°C cooler

TABLE 5. Mean LAI (± SD) for grasses, forbs and shrubs in the spring, summer and autumn burns at the end of the 1999 growing season (cm^2 cm^{-2}).

	Control	Spring	Summer	Autumn
Grasses	$0.64 \pm 0.14^{a*}$	0.41 ± 0.04^{ab}	0.28 ± 0.04^{b}	0.27 ± 0.07^{b}
Forbs	0.09 ± 0.02^{a}	0.23 ± 0.05^{a}	0.18 ± 0.02^{a}	0.13 ± 0.06^{a}
Shrubs	0.27 ± 0.06^{a}	0.04 ± 0.02^{ab}	0.15 ± 0.03^{ab}	0.50 ± 0.11^{b}

*Values in the same row with the same letter are not significantly different ($P \leq 0.05$)

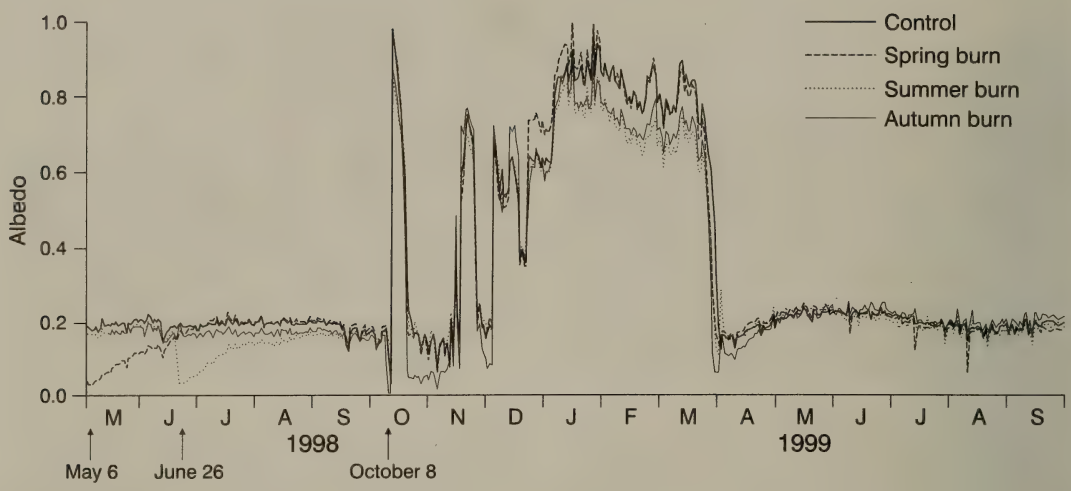


FIGURE 5. Daily albedos in the control and spring, summer and autumn burns.

than the control. In the second growing season the 10 cm soil temperatures in the spring and summer plots were about 1.5°C warmer than the control; in comparison the autumn plot was about 2.5°C warmer with the mean temperature in August reaching 18.6°C. This is similar to the 3°C increase in burned tallgrass prairie reported by Rice and Parenti (1978). In the first growing season mean monthly soil temperatures at 50 cm increased to a maximum of 17.9°C in the summer plot in August compared to maximum values of 15.4°C in the control and 15.1°C and 16.7°C, respectively, for the autumn and spring burns (Figure 6). By mid-winter the mean 50 cm soil temperature in the autumn burn had dropped to -7.3°C, which was about 2.5°C colder than the other burned plots and almost 4°C colder than the control. Differences in 50 cm soil temperatures were less marked in the second growing season.

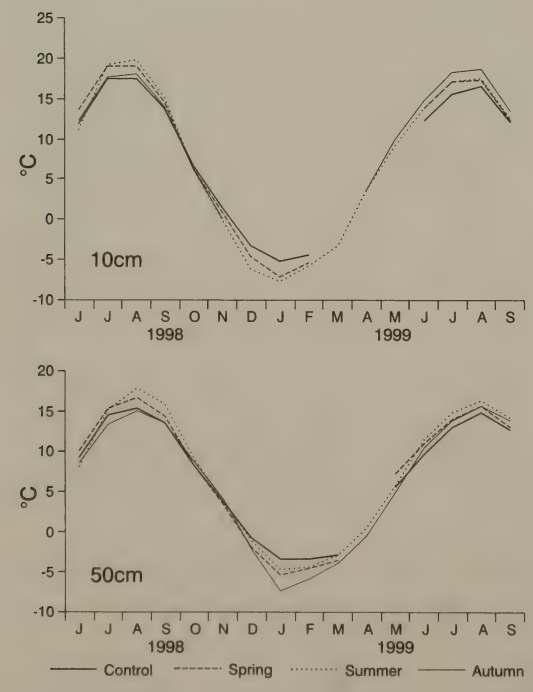


FIGURE 6. Mean monthly soil temperatures at 10 cm and 50 cm in the control and spring, summer and autumn burns.

Temperature differences between plots may be attributed to the insulating effect of the litter and snow cover. A mulch of litter helps to reduce loss of both sensible and latent heat as well as radiative heat loss from the soil. Kohnke and Werkhoven (1963) demonstrated that soil temperature at a depth of 10 cm was the same as that recorded at 2.5 cm under a straw mulch of 0.38 kg m^{-2}. Similarly, Unger (1978) reported that winter soil temperatures increased by approximately 0.1°C for each 0.1 kg of straw mulch applied. Snow provides better insulation for strawberry plants than straw mulch under severe winter conditions (Boyce and Linde 1986). The thermal diffusivity of straw is about 5×10^{-6} m^2s^{-1} and ranges from 4×10^{-7} m^2s^{-1} for fresh snow to over 5×10^{-7} m^2s^{-1} for a mature snowpack (List 1966). In addition, solar radiation will penetrate a translucent snowpack and provide a net radiative heat gain (Marchand 1984; Oke 1978). Water vapor also moves upwards from the deep warmer soil towards the colder surface and releases latent heat when it condenses. If snow arrives before freezing occurs, some of this heat is retained within the soil.

At the end of the first growing season, water content was highest in the control and decreased progressively

TABLE 6. Soil water content (mm) of the control and treatment plots during the 1998 and 1999 growing seasons measured by neutron probe.

	1998 growing season	1999 growing season
Precipitation	248	270
Control	+13	-9
Spring burn	-17	-3
Summer burn	-5	-6
Autumn burn	+29	-8

in the autumn, spring and summer burns (Figure 7). The drier soils in the spring and summer plots are attributed to a combination of increased soil evaporation due to loss of canopy and mulch and to high water demand from vigorous regrowth; the autumn plot would have lost moisture mainly through transpiration. Moisture levels increased in April as snowmelt percolated into the soil. At this time the greatest moisture reserves occurred in the control and the autumn burn was the driest. This pattern is consistent with observations made by de Jong (1973) and Trlica and Schuster (1969) who reported low soil moisture levels in grasslands that had been burned in the autumn. Such differences can be attributed to lower infiltration rates, reduced winter snow-trapping and to microclimatic effects (McMurphy and Anderson 1965; Redmann 1978). In the present study the mid-February snow cover differed significantly ($P \leq 0.01$) between plots with snowpack water equivalents of 73 mm, 48 mm, 35 mm, and 25 mm in the control, spring, summer, and autumn burns, respectively. Trlica and Schuster (1969) found a similar reduction in snow cover in autumn burned grassland because the snow is more easily removed by wind. Neutron probe data (Table 6) to a depth of 1.0 m indicated that during the summer of 1998 the spring burn lost 265 mm of water compared to 253 in the summer burn 235 mm in the control and 219 mm in the autumn burn. During 1999 the difference in soil water loss was about 275 mm for all plots which is 56% to 71% of values reported for tallgrass prairie in Oklahoma (Burba and Verma 2001).

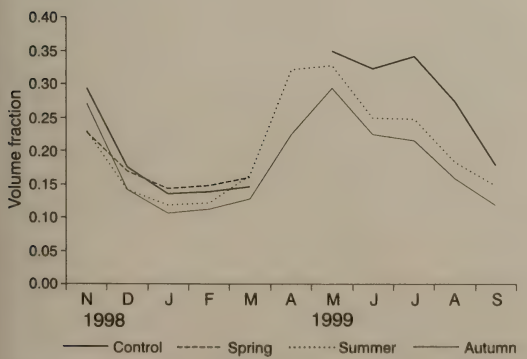


FIGURE 7. Mean monthly Time Domain Reflectometry soil water values in the control and spring, summer and autumn burns.

Many cool season plants, such as those monitored in this study, grow actively during the spring and summer so are affected directly by burning during these seasons. At all times fire removes part or most of the plant canopy, changing surface albedo and radiation exchange, air flow and snow trapping, soil temperature and plant and soil water loss. These effects disappear rather quickly, however, after a single burning episode so that there is little long-term impact on the vegetation. Repeated burnings are likely to have long-term impacts but this was not investigated in this study.

Acknowledgments

The authors thank Garth Wruck for assisting with the vegetation surveys, Hong Mei Li for helping with laboratory work and Keith Bigelow for drawing the figures. We also appreciate the co-operation of the Department of Plant Sciences, University of Saskatchewan for allowing access to Kernen Prairie.

Literature Cited

Anderson, K. L. 1965. Time of burning as it affects soil moisture in an ordinary upland bluestem prairie in the Flint Hills. Journal of Range Management 18: 311-316.

Anderson, K. L., E. F. Smith, and **C. E. Owensby.** 1970. Burning bluestem range. Journal of Range Management 23: 81-92.

Archibold, O. W., L. J. Nelson, E. A. Ripley, and **L. Delanoy.** 1998. Fire temperatures in plant communities of the northern mixed prairie. Canadian Field-Naturalist 112: 234-240.

Atmospheric Environment Service. 1993. Canadian Climate Normals 1961-90 – Prairie Provinces. Environment Canada, Minister of Supply and Services Canada, Ottawa, Ontario.

Atmospheric Environment Service. 1998-1999. Monthly Meteorological Summaries – Saskatoon International Airport, Prairie and Northern Region. Environment Canada, Winnipeg, Manitoba.

Bailey, A. W., and **M. L. Anderson.** 1980. Fire temperatures in grass, shrub and aspen forest communities of central Alberta. Journal of Range Management 33: 37-40.

Baines, G. B. K. 1973. Plant distributions on a Saskatchewan prairie. Vegetatio 28: 99-123.

Bowers, S. A., and **R. J. Hanks**. 1965. Reflection of radiant energy from soils. Soil Science 100: 130-138.

Boyce, B. R., and **A. W. Linde.** 1986. A comparison of manmade snow, natural snow and straw mulch for winter protection of strawberry plants. Advances in Strawberry Production 5: 25-27.

Bremer, D. J., and **J. M. Ham.** 1999. Effect of spring burning on the surface energy balance in a tallgrass prairie. Agricultural and Forest Meteorology 97: 43-54.

Burba, G. R., and **S. B. Verma.** 2001. Prairie growth, PAR albedo and seasonal distribution of energy fluxes. Agricultural and Forest Meteorology 107: 227-240.

Clarke, S. E., E. W. Tisdale, and **N. A. Skoglund.** 1943. The effects of climate and grazing practices on short-grass prairie vegetation in southern Alberta and southwestern Saskatchewan. Canada Department of Agriculture Technical Bulletin 46.

Daubenmire, R. 1968. Ecology of fire in grasslands. Advances in Ecological Research 5: 209-266

De Jong, E. 1973. Soil physics II. Soil water. Matador Project Technical Report 29. University of Saskatchewan, Saskatoon.

De Jong, E., and **K. B. Macdonald.** 1975. Soil moisture regime under native grassland. Geoderma 14: 207-221.

Dix, R. L. 1960. The effects of burning on mulch structure and species composition of mixed grasslands in western North Dakota. Ecology 41: 49-56.

Engle, D. M., and **P. M. Bultsma.** 1984. Burning of northern mixed prairie during drought. Journal of Range Management 37: 398-401.

Ewing, A. L., and **D. M. Engle.** 1988. Effects of late summer fire on tallgrass prairie microclimate and community composition. American Midland Naturalist 120: 212-223.

Knapp, A. K. 1984. Post-burn differences in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. American Journal of Botany 71: 220-227.

Kohnke, H., and **C. H. Werkhoven.** 1963. Soil temperature and soil freezing as affected by an organic mulch. Soil Science Society of America Proceedings 27: 13-17.

List, R. J. 1966. Smithsonian Meteorological Tables. Smithsonian Institute, Washington, D. C.

Marchand, P. J. 1984. Light extinction under a changing snowcover. Carnegie Museum of Natural History, Special Publication 10: 33-37.

Martin, R. E., C. T. Cushwa, and **R. L. Miller.** 1969. Fire as a physical factor in wildland management. Pages 271-288 *in* Proceedings of the 9th Annual Tall Timbers Fire Ecology Conference.

McMurphy, W. E., and **K. L. Anderson**. 1965. Burning Flint Hills range. Journal of Range Management 18: 265-269.

Oke, T. R. 1978. Boundary Layer Climates. Methuen, London.

Old, S. M. 1969. Microclimate, fire and plant production in an Illinois prairie. Ecological Monographs 38: 355-383.

Peet, M., R. Anderson, and **M. S. Adams.** 1975. Effect of fire on big bluestem production. American Midland Naturalist 94: 15-26.

Pylypec, B. 1986. The Kernen Prairie – a relict fescue grassland near Saskatoon, Saskatchewan. Blue Jay 44: 222-231.

Raby, S. 1966. Prairie fires in the northwest. Saskatchewan History 19: 81-99.

Redmann, R. E. 1978. Plant and soil water potentials following fire in a northern mixed grassland. Journal of Range Management 31: 443-445.

Redmann, R. E., J. T. Romo, B. Pylypec, and **E. A. Driver.** 1993. Impacts of burning on primary productivity of *Festuca* and *Stipa-Agropyron* grasslands in central Saskatchewan. American Midland Naturalist 130: 262-273.

Rice, E. L., and **R. L. Parenti.** 1978. Causes of decreases in productivity in undisturbed tall grass prairie. American Journal of Botany 65: 1091-1097.

Romo, J. T., P. L. Grilz, R. E. Redmann, and **E. A. Driver.** 1993. Standing crop, biomass allocation patterns and soil-plant water relations in *Symphoricarpos occidentalis* Hook. following autumn or spring burning. American Midland Naturalist 130: 106-115.

Steuter, A. A. 1987. C3/C4 production shift on seasonal burns – northern mixed prairie. Journal of Range Management 40: 27-31.

Tester, J. R. 1965. Effects of a controlled burn on small mammals in a Minnesota oak-savanna. American Midland Naturalist 74: 240-244.

Toynbee, K. 1987. Prolific flowering year for Plains Rough Fescue at Kernen Prairie. Blue Jay 45**:** 142-143.

Trlica, M. J., and **J. L. Schuster.** 1969. Effects of fire on grasses of the Texas high plains. Journal of Range Management 22: 329-333.

Unger, P. W. 1978. Straw mulch and sorghum. Agronomy Journal 70: 858-864.

Vogl, R. J. 1974. Effects of fires on grasslands. Pages 139-194 *in* Fire and Ecosystems. *Edited by* T. T. Kozolowski and C. E. Ahlgren. Academic Press, New York.

White, R. S., and **P. O. Currie**. 1983. Prescribed burning in the northern Great Plains: Yield and cover responses of 3 forage species in the mixed grass prairie. Journal of Range Management 36: 179-183.

Wright, H. A., and **A. W. Bailey.** 1980. Fire ecology and prescribed burning in the Great Plains – a research review. U.S. Forest Service General Technical Report INT-77.

Received 17 June 2002
Accepted 8 December 2003

Density and Richness of Benthic Invertebrate Populations in the North Sydenham River of Southwestern Ontario (1996-2000) Compared with Those of the St. Clair River (1990-1995)

I. W. E. Harris[1], C. F. Drury[2], R. R. Simard[3], and T. Q. Zhang[2]

[1] 1310 Hillcrest Drive, Sarnia, Ontario N7S 2N4 Canada
[2] Greenhouse and Processing Crops Research Centre, Agriculture and Agri-Food Canada, Harrow, Ontario N0R 1G0 Canada
[3] Soils and Crops Research and Development Centre, Agriculture and Agri-Food Canada, Ste. Foy, Québec G1V 2J3 Canada

Harris, I. W. E., C. F. Drury, R. R. Simard, and T. Q. Zhang. 2003. Density and richness of benthic invertebrate populations in the North Sydenham River of Southwestern Ontario (1996-2000) compared with those of the St. Clair River (1990-1995). Canadian Field-Naturalist 117(2): 267-277.

Richness (the number of invertebrate families/sample site) and density (the number of invertebrates/sq m) of benthic populations in the North Sydenham River were measured and compared with similar estimates for the St. Clair River. Seventeen sample sites were examined from May to October over five consecutive years. At each sample site, particle size distribution of the sediment, sediment temperature, total phosphorous, total nitrogen, total carbon, and water flow rate were measured. Physical and chemical characteristics of the North Sydenham system over the 100 km run examined were less variable than those of the St. Clair. Statistically significant but weak multiple linear correlations were found for richness and density with several of the measured variables. Invertebrate populations in the North Sydenham River were less rich and less dense than those in the downstream reach of the St. Clair and exhibited a different distribution of abundance among the orders of organisms. As in the St. Clair River, some evidence of long term cycling of abundance in several families of invertebrates was found in the North Sydenham.

Key Words: benthic invertebrates, richness, density, North Sydenham River, Southwestern Ontario, sediments, nitrogen, phosphorous, organic debris, St. Clair River.

In 1996 a five-year study was undertaken to identify some major variables correlating with the richness and density of invertebrate populations in the sediments of the North Sydenham River in Southwestern Ontario. This work should be viewed as complementary to the similar study of invertebrates in the St. Clair River for the 1990-1995 period (Harris 1999). The comparison of the populations in these two streams will provide base-line data for assessing the effectiveness of remedial actions underway in the Sydenham River system (Whitford 2001*) and in the St. Clair as required by the International Joint Commission (I.J.C.) Great Lakes Water Quality Agreement (1987*). Furthermore, comparable invertebrate data for streams of such widely differing characteristics will assist in the interpretation of the effects of physical and chemical variables on invertebrate populations in other river systems (Statzner and Higler 1986; Meyer 1990). Although a few studies focussed on Bivalvia have been reported for the Sydenham River System as a whole (Mackie and Topping 1988; Clarke 1992; VanDerWal 2001*), no comprehensive studies of the invertebrate population in the North Sydenham branch have been published.

Study Site

The North Sydenham River is the major northern branch of the Sydenham River in Southwestern Ontario, flowing northeast-southwest and entering the main stream at the town of Wallaceburg. The Sydenham River then continues south-westerly to the Chenal Ecarte, the eastern channel in the delta of the St. Clair River in Lake St. Clair (Figure 1).

The North Sydenham is a third order stream flowing through agricultural land which supports crops of soybeans, corn, hay and various grains as well as cattle, hogs and poultry. In some sections deciduous trees and brush overhang the stream. The stream bed is a glacial clay and with the variable flows resulting from periodic heavy rains, field-tile drainage, and cattle access, the water carries suspended solids varying between 125 mg/l in the lower reach to 55 mg/l in the upper portions of the system (Chambers 1997*). Comparable data for the shoreline stream of the St. Clair River are normally in the range 1-10 mg/l with one to three periods per year with values as high as 30 mg/l for a week or two following storms on Lake Huron (Frais 2002*). The water in the North Sydenham is opaque at depths of more than about one centimetre and turbidity has been reported in the range 50-75 Jackson Turbidity Units (Whitford 2001*). The nearshore water of the St. Clair River is clear most of the time and the bottom can be seen at depths up to three metres. The course of the North Sydenham is sufficiently convoluted that about 100 kilometres is required to traverse a straight line distance of about 50 kilometres. The overall bed gradient is 0.0003.

In the lower reaches of the North Sydenham River, historical data show that flow is normally in the range of six to sixteen cubic metres per second during the

summer months (McDougall 1998*), occasionally reaching thirty cubic meters per second in the early spring. The Bear Creek/Durham Creek tributary system contributes about twenty percent of this flow and the Black Creek/Fox Creek tributary contributes about seventy percent. Several small tributaries account for the remainder. In the latter half of the summer, at distances more than sixty kilometres upstream, flow is negligible, and the stream becomes a series of long narrow ponds most of the time.

Historical data (McDougall 1998*) for the North Sydenham River show a peak water temperature of about 24°C at the end of June (weeks 26-27). Comparable data for the St. Clair River (Kuley and Brooks 2001*) show a peak at about 22°C in mid-August (weeks 32-33). Sediment temperatures were not measured in the St. Clair River study.

Materials and Methods

Twelve parameters were considered to be independent variables having the potential to be correlated at a statistically significant level with the richness and density of invertebrate populations in the river as follows:

year	five years between 1996 and 2000 including (96, 97, 98, 99, 100).
weekno	sampling week (weeks numbered from the first week in January of each year).
riverkm	nominal stream distance in kilometres measured upstream of the base point at the junction of the North Sydenham River with the main flow at Wallaceburg.
ms	river surface flow rate at the time and point of sampling (metres/sec).
vg	gravel content of sediment sample — volume percent of inorganic material having a particle size > 2.0 mm.
vs	sand content of sediment sample — volume percent of inorganic material having a particle size between 2.0 mm and 0.2 mm.
vm	mud content of sediment sample — volume percent of inorganic material having a particle size < 0.2 mm.
vv	vegetation content of sediment sample — volume percent of macrophytic material on the 2 mm screen.
pμgg	total phosphorous content of sediment expressed as micrograms/gram.
nμgg	total nitrogen content of sediment expressed as micrograms/gram.
cμgg	total carbon content of sediment expressed as micrograms/gram.
sedtc	temperature of sediment at the point and time of sampling expressed as degrees Celsius.

Total carbon content (cugg) and sediment temperature (sedtc) were not measured in the St. Clair River study (Harris 1999). The volume percent variables are obviously interrelated since they must sum to one hundred. However, the analysis of the data by multiple linear regression identifies the classes of sediment particle size which are statistically significant in the correlations. The dependent variables in the analysis of the data were:

richness	number of invertebrate families found at each site.
density	total of invertebrate individuals found at each site expressed as number m^2.

Seventeen sample points were established along the lower section of the river, Bear Creek, Durham Creek, Fox Creek, and Black Creek as shown in Figure 1. For ease of sampling and to minimize the risk of contamination by storm drainage, all were located about 20 m upstream of road bridges over the streams. The geographic coordinates for all sample points are listed in Table 1. Only that part of the North Sydenham system lying within the Townships of Enniskillen, Plympton, Moore, and Sombra of the County of Lambton was included in this study. Nine of the 17 sampling sites in this study were located adjacent to cultivated fields or pasture; the remainder were bordered with willow brush and/or deciduous trees.

Samples were taken at a depth of 1 m about 2 m from the shore or in midstream in the upper reaches where the stream was shallow and narrow. Each site was sampled once each year between May and October for the period 1996 through 2000. As illustrated in Figure 2, a schedule was established to ensure that samples were taken during the five-year study at each site over as wide a seasonal range as possible with a minimum of duplication.

Sampling for invertebrate identification at each site consisted of three grabs with a Petit Ponar dredge (0.0234 m^2) the contents of which were combined, washed on a screen with 0.5 mm mesh, and preserved in 2% formaldehyde. The invertebrates present were subsequently separated by hand under magnification from the sediment debris, identified to the family level, counted and preserved in 70% isopropanol containing 0.2% glycerin. Empty shells and exuviae were not counted. Identification of invertebrates followed keys published by Merritt and Cummins (1988), Pennak (1989), Peckarsky et al. (1990) and Thorp and Covich (1991).

An archive of all specimens found, in vials coded with invertebrate order, sample site, and sampling date was accumulated to allow verification of invertebrate identification and counts. All these specimens have been deposited in the Zoology Department of the University of Western Ontario (Robert Bailey).

At each sampling, a fourth grab of sediment was taken to characterize the distribution of particle sizes in the sediment. Following consultation with the Geology Department at the University of Western Ontario, an arbitrary decision was made to use screens with openings of 2 mm and 0.2 mm and a graduated cylinder to measure the volume percent of gravel, sand and mud respectively. When present, the volume percent of macrophytic debris was estimated visually from the residue on the 2 mm screen and the volume percent gravel corrected accordingly.

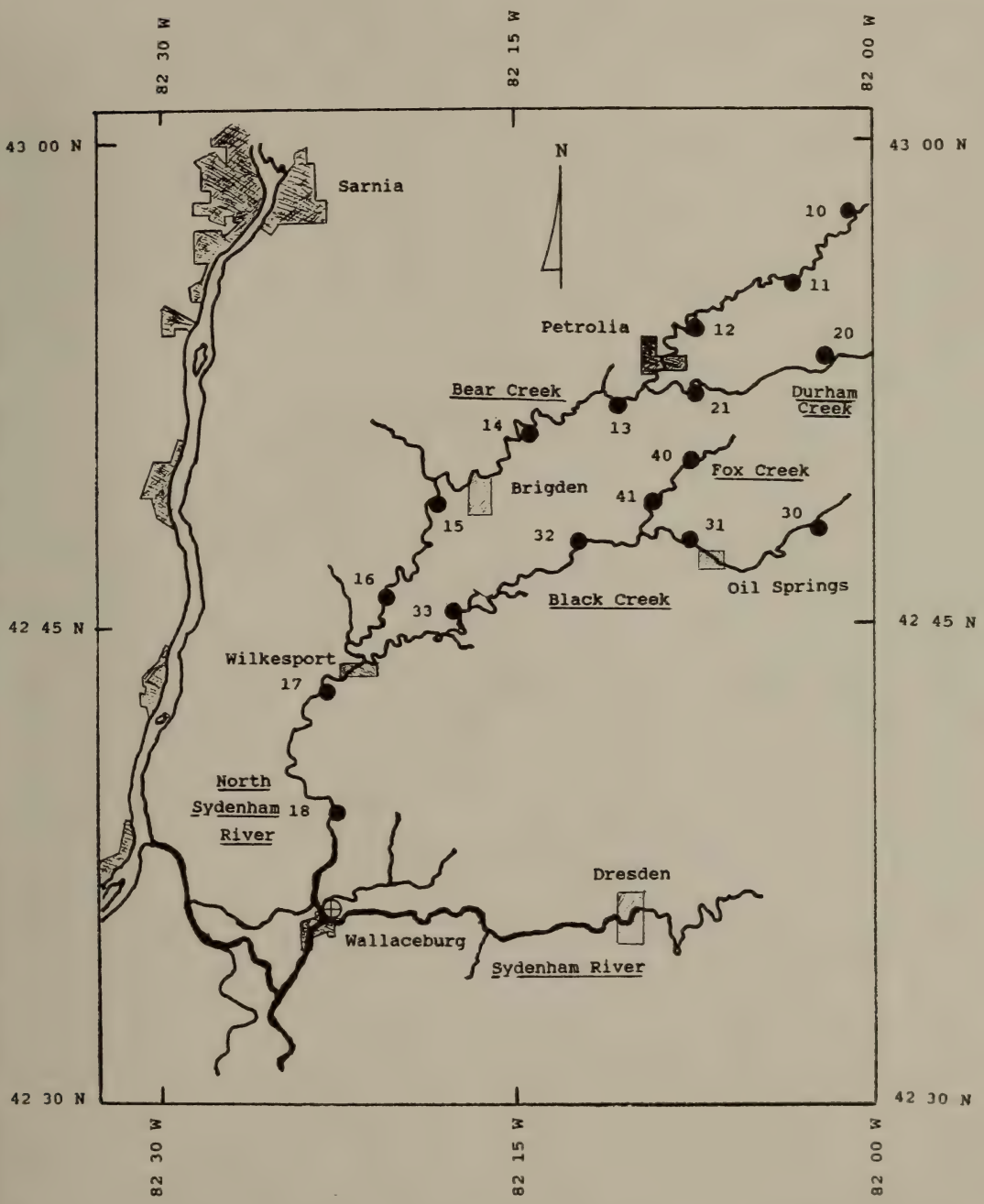


FIGURE 1. The North Sydenham River system and the adjacent St. Clair River showing the location of the sampling points (numbered).

A fifth grab sample of sediment was taken at each sampling for analysis for total nitrogen, total phosphorous and total carbon. The analyses were performed in the laboratories of Agriculture and Agri-Food Canada at Harrow, Ontario and Ste. Foy, Quebec.

Current velocity (metres/sec) at the surface was measured by timing the passage of a wooden float over a fixed distance. Sediment temperature was measured by probing the stream bottom with a thermometer to a depth of about 5 cm.

TABLE 1. Coordinates for stream monitoring sites.

Site Name	Site Number	Nominal River Km *	Latitude(N) Deg.	Min. +	Sec.	Longitude(W) Deg.	Min. +	Sec.
BEAR CREEK/DURHAM CREEK TRIBUTARIES:								
Bear Creek	10	106.5	42	57	20	82	0	40
Bear Creek	11	96.7	42	55	25	82	3	0
Bear Creek	12	84.8	42	53	50	82	7	30
Bear Creek	13	72.4	42	51	50	82	11	0
Bear Creek	14	59.4	42	51	0	82	14	30
Bear Creek	15	45.7	42	48	50	82	18	0
Bear Creek	16	34.4	42	45	40	82	20	50
Durham Creek	20	95.9	42	52	50	82	1	10
Durham Creek	21	80.1	42	51	50	82	7	40
BLACK CREEK/FOX CREEK TRIBUTARIES:								
Black Creek	30	77.2	42	47	50	82	2	0
Black Creek	31	64.8	42	47	20	82	8	20
Black Creek	32	53.7	42	47	10	82	12	0
Black Creek	33	40.0	42	45	10	82	17	0
Fox Creek	40	69.2	42	49	40	82	8	20
Fox Creek	41	63.8	42	48	30	82	7	30
NORTH SYDENHAM:								
North Sydenham	17	20.3	42	42	40	82	22	40
North Sydenham	18	7.8	42	39	0	82	22	30

* distance measured upstream from Wallaceburg
+ maps published by Energy Mines and Resources Canada.1987. Maps number 40-J/9, 40-J/10, 40-J/16, 40-O/1.

The data were analysed using software developed by the Centers for Disease Control and Prevention (CDC) in Atlanta, Georgia, USA (titled EpiInfo, Version 6). A diskette containing the entire database can be obtained from the author at no charge. If required, the data base can be reformatted for several other commercial software systems.

Results and Discussion

To simplify the presentation of the findings of this study, data for the two tributary systems of the North Sydenham River have been grouped and recorded in Table 2 as arithmetic means with associated statistical characteristics. Also recorded for comparison are data for the downstream reach of the St. Clair River (Harris 1999). Significance of the difference between many of these means is indeterminate because of significant differences between the variances. However, some observations of interest are as follows:

(i) at the 95% level of confidence, the lower reach of the North Sydenham River shows a higher population density than the Bear Creek/Durham Creek tributary system but is not significantly different from the downstream reach of the St. Clair River. The significance of the difference for the Black Creek/Fox Creek system is indeterminate because of the difference of variances.

(ii) the lower reach of the North Sydenham River shows a significantly higher richness than both tributary systems.

(iii) mean sediment temperatures of all reaches of the North Sydenham system do not differ. As with the water, the sediment temperature profile is parabolic during the summer months. However, the maximum occurs at about 22°C in mid-July (weeks 28-30), about two degrees lower and two weeks later than the water temperature (McDougall 1998*).

(iv) the sediment of the Black Creek/Fox Creek tributary system has a higher proportion of gravel than either the Bear Creek/Durham Creek system or the downstream main portion of the river. These differences are significant at the 95% level of confidence. The gravel content for all three appears to be higher than for the downstream reach of the St. Clair but the statistical significance of that difference is indeterminate because of variance differences.

(v) the sand content of the sediment throughout the North Sydenham River is the same and about half that in the downstream reach of the St. Clair but the statistical significance of the latter difference is indeterminate.

(vi) the proportion of mud in all sediments is the same.

(vii) the proportion of gross organic debris in the Black Creek/Fox Creek system is lower than in either of the other two segments of the river at the 95% level of confidence.

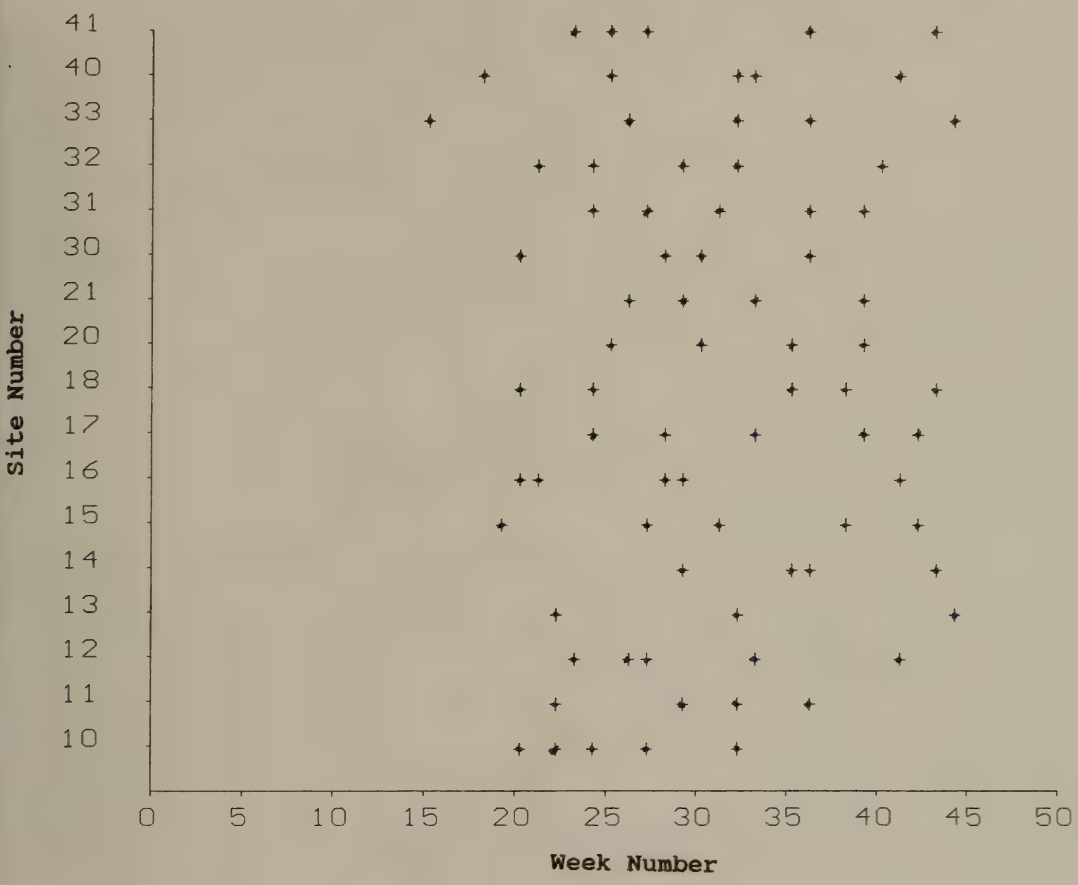


FIGURE 2. The sampling schedule for the period 1996-2000.

(viii) the phosphorous content of the sediments throughout the North Sydenham River is the same and about twice that in the lower St. Clair River. However, the N/P ratios of the sediments in both systems are in the range of 2.5 to 3.0. The N/P ratio of the water in the North Sydenham has been found to be about 8 (Chambers 1997*).

(ix) the Black Creek/Fox Creek tributary system sediments contain levels of nitrogen lower, at 95% confidence, than the other two segments of the system but the nitrogen level in the downstream reach of the St. Clair River is lower still.

(x) the sediment in the Bear Creek/Durham Creek tributary system contains significantly more carbon than the other two parts of the river. The C/N ratio in the North Sydenham system as a whole is in the range 30 to 35.

The higher values of density and richness in the downstream reach of the North Sydenham River relative to the tributary systems and the absence of a consistent pattern of values in the other stream characteristics indicate that none of the measured variables exert a major influence on either richness or density of invertebrate populations. This observation is reinforced when the data for the St. Clair River are considered as well.

The mean values for richness, recorded in Figure 3 which decline with passage upstream, follow the normal pattern observed in numerous stream studies (Waters 1972; Williams 1981) as well as the recent study on the St. Clair River (Harris 1999).

The data in Figure 4 for population density show little evidence of a trend with passage upstream in contrast to the marked decline observed in the upper reach of the St. Clair River.

Error bars have been omitted from Figures 3, 4, and 5 because they would include variation of all the measured variables except river distance and would therefore be misleading. Further, the figures would be very difficult to read. These figures are presented to illustrate trends rather than precision.

To examine further the significance of the independent variables on richness and density, multivariate linear regressions (Draper and Smith 1991) were run repeatedly for both using all data from all sites for

TABLE 2. Arithmetic means of basic river characteristics and corresponding density and richness of benthic invertebrate populations in the North Sydenham River and the downstream reach of the St. Clair River (Harris 1999).

	Density (org.m^2) *	Richness (fam./site) *	Sediment Temp. (C) *	Sediment Character vg *	vs *	vm *	vv *	Nutrient pug *	nugg *	Carbon cugg *
Bear Creek/Durham Creek Tribuaries (Siteno 10-16,20,21):										
Mean	2447.8	9.7	19.0	15.0	24.0	43.0	17.9	590.8	1453.7	48423
Observations (n)	42	42	42	42	42	42	42	42	42	42
Standard Error	419.1	0.5	0.5	2.8	2.6	4.4	3.3	18.4	124.2	2045
Variance	7.4E+6	9.6	11.1	317.6	282.6	831.6	452.8	1.4E+4	0.6E+6	1.8E+8
Black Creek/Fox Creek Tributaries (Siteno 30-33,40,41):										
Mean	2408.1	10.8	18.9	23.8	20.4	46.0	9.9	554.9	1170.8	41107
Observations (n)	29	29	29	29	29	29	29	29	29	29
Standard Error	299.7	0.7	0.6	3.3	2.5	4.2	3.3	16.8	93.2	2200
Variance	2.6E+6	15.9	10.7	321.8	176.3	508.1	311.8	0.8E+4	0.2E+6	1.4E+8
North Sydenham River (Siteno 17,18):										
Mean	4796.8	14.2	19.6	13.7	21.4	46.7	18.4	582.0	1475.6	43640
Observations (n)	10	10	10	10	10	10	10	10	10	10
Standard Error	797.3	0.7	1.0	4.6	3.3	7.0	6.2	52.4	289.3	2736
Variance	6.4E+6	5.5	10.0	208.4	112.5	489.8	378.9	2.7E+4	0.8E+6	0.7E+8
St. Clair River (Siteno 009,010,106,107,108):										
Mean	5067.4	18.9	–	4.5	41.0	42.4	11.9	291.1	812.7	–
Observations (n)	21	21	–	21	21	21	21	21	21	–
Standard Error	577.0	1.2	–	1.1	5.7	6.4	2.5	15.6	75.3	–
Variance	7.0E+6	32.2	–	25.5	686.9	856.8	132.5	0.5E+4	0.1E+6	–

* abbreviations defined in Materials and Methods section

the entire five-year period. Initially in each case, all independent variables were included in the calculation. In successive runs, the independent variable with least significance was eliminated until only those with B coefficients significant at the 95% level remained. The numerical data for the final correlations are recorded in Table 3. Richness and density in both arithmetic and log form were run to assess the effect of the marked positive skewness of these data. The final correlation for density in arithmetic form did not reach significance at the 95% level of confidence. The procedure here is the same as that used in the St. Clair River study.

This analysis revealed the following equations to be significant at the 95% level:

Richness = 12.9 + 0.561(vv) + 0.007(pugg)
- 0.048(riverkm) - 0.210(sedtc)
Correlation coefficient (r^2) = 0.36

Log(Richness) = 0.78 + 0.003(vv) + 0.0003(pugg)
- 0.002(riverkm) + 0.004(weekno)
Correlation coefficient (r^2) = 0.32

Log(Density) = 2.72 + 0.005(vv) + 0.015(weekno)
Correlation coefficient (r^2) = 0.10

All these correlations, although statistically significant at the 95% level, are weak in that they account for only a small proportion of the total variation in the richness and density observed. The corresponding correlations found in the St. Clair River study (Harris 1999) were much more robust, being in the range of 40%-60%. Apparently, variables other than those measured are influential; perhaps for example, water clarity or the daily temperature variation.

The weakness of these correlations is also attributable in part to the narrower ranges in the measured independent variables in the North Sydenham compared to those in the St. Clair River. Except for the amounts of coarse vegetation debris (vv) and the longer upstream distance (riverkm), the ranges for the independent variables in the North Sydenham are about half those observed in the St. Clair River. In other words, the North Sydenham River is a much more homogeneous environment than the St. Clair.

It should be emphasised that these are correlations and not necessarily demonstrations of cause and effect. For example, the positive effect of the presence of coarse vegetation debris on both richness and density could be either that it provides cover for invertebrates

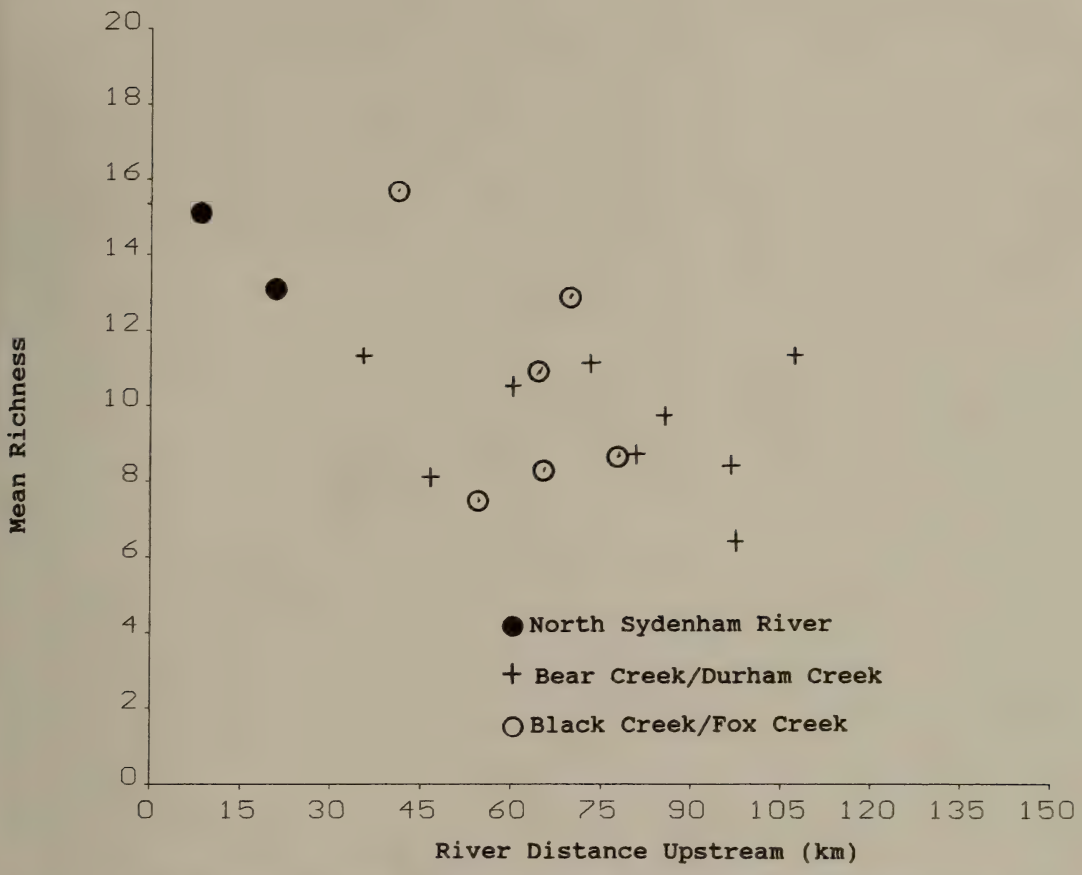


FIGURE 3. Mean richness (number of invertebrate families/site) plotted against distance upstream (km).

from predators, that it provides nutrient, or that the presence of overhanging trees and brush provides a more undisturbed stream bed.

Nevertheless, richness is shown to be favoured by the presence of coarse vegetation debris, higher levels of phosphorous, lower sediment temperatures, and by sampling farther downstream later in the year. Density tends to be increased by sampling later in the year at sites where coarse vegetation debris is present. The presence of such material is known to provide refuge and nutrients for invertebrates (Dudley and Anderson 1982). The negative association with coarse vegetation found in the St. Clair River study remains anomalous.

It should be noted here that the coarse vegetation debris found in the North Sydenham River is very different from that found in the St. Clair. In the North Sydenham it is composed of leaf litter and decaying wood. In the St. Clair, when present, it is mainly growing macrophytes (*Chara* spp. and *Potamogeton* spp.).

In contrast to the findings in the St. Clair River study, richness in the North Sydenham exhibited no yearly trend. No yearly trend in density was observed in either river system.

Evidence for cycling in the abundance of some invertebrate families observed in the study of the St. Clair was also found in the North Sydenham study. Table 4 records this evidence. A comparison with the comparable data from the St. Clair River study (Harris 1999) suggests that the more lentic environment of the North Sydenham supports a more constant invertebrate population exhibiting cycles of density having smaller amplitude and longer periods. The population in a pond environment would therefore be expected to exhibit cycles with even smaller amplitude and longer periods. The evidence for long term cyclic variation in the density of some invertebrate families suggests that studies of the abundance of invertebrate populations in a river system or pond must be conducted over a consecutive period of years if the results are to be credible.

The abundance of individuals in the various orders of invertebrates found in the North Sydenham River compared to the St. Clair River is recorded in Table 5. Because the distributions of the data for each order

TABLE 3. Regression analyses for richness and density.

RICHNESS
Correlation coefficient: r^2 = 0.36

Variable	Mean	B coefficient	95% confidence Lower	95% confidence Upper	Std Error	Partial F-test
VV	15.11	0.0561	0.021	0.091	0.018	10.28
PUGG	576.86	0.0067	0.001	0.013	0.003	5.14
RIVERKM	61.99	-0.0480	-0.074	-0.022	0.013	13.76
SEDTC	18.89	-0.2102	-0.419	-0.001	0.105	4.02
Y-Intercept	12.871					

LOG (RICHNESS)
Correlation coefficient: r^2 = 0.32

Variable	Mean	B coefficient	95% confidence Lower	95% confidence Upper	Std Error	Partial F-test
VV	15.11	0.0026	0.001	0.004	0.001	11.02
PUGG	576.86	0.0003	0.000	0.000	0.000	4.21
RIVERKM	61.99	-0.0016	-0.003	-0.000	0.001	8.33
WEEKNO	30.41	0.0043	0.000	0.008	0.002	4.21
Y-Intercept	0.781					

LOG (DENSITY)
Correlation coefficient: r^2 = 0.10

Variable	Mean	B coefficient	95% confidence Lower	95% confidence Upper	Std Error	Partial F-test
VV	15.11	0.0053	0.000	0.010	0.002	4.84
WEEKNO	30.41	0.0151	0.002	0.028	0.007	5.18
Y-Intercept	2.718					

exhibited a marked positive skewness, geometric means are presented here to give a more accurate picture of relative frequency than that provided by arithmetic means.

Statistically significant differences at the 95% level of confidence are noted for Diptera, Ephemeroptera, Bivalvia, Trichoptera, and Amphipoda. All are less frequent in the North Sydenham River. Other differences are either not statistically significant or indeterminate because of differences in variance. The low number of Gastropoda is attributable to the relative absence of both hard substrate and algal growths in the North Sydenham. The high number of Coleoptera (mainly Elmidae) relative to that in the St. Clair River is a salient feature probably attributable to the widespread presence of decomposing woody material (Dudley and Anderson 1982). Other factors probably contributing to the differences between the two river systems are the high sediment load of the water in the North Sydenham and the different temperature environment (Ward 1986; Hynes 1970).

TABLE 4. Yearly mean density of selected families. All sites combined.

North Sydenham River (this study)

Year	Chironomidae	Gammaridae	Caenidae	Naididae
1996	1752	180	419	1709
1997	2222	111	325	2538
1998	2423	8	188	3256
1999	1855	21	290	2440
2000	1483	43	453	1487

St. Clair River (Harris 1999)

Year	Chironomidae	Gammaridae	Caenidae	Dreisseniidae
1990	436	483	13	0
1991	1124	158	34	26
1992	2226	103	205	103
1993	4996	47	278	1038
1994	4397	56	141	68
1995	5607	51	77	8

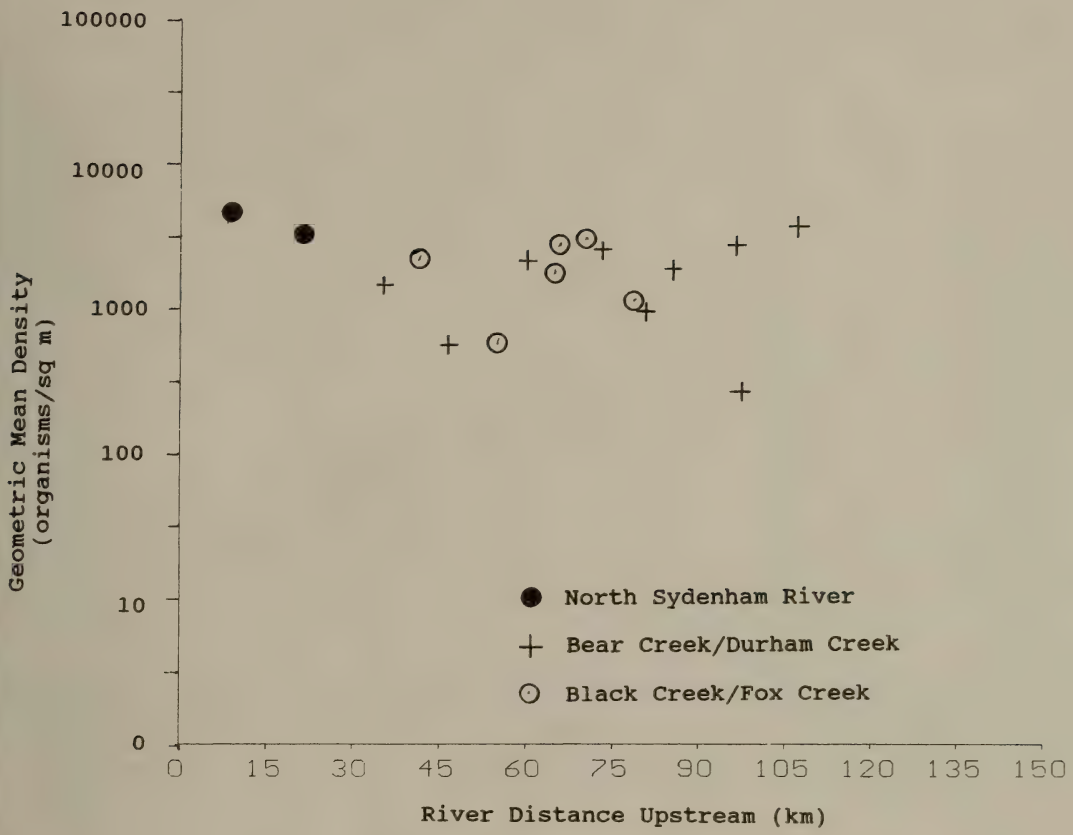


FIGURE 4. Geometric mean density (organisms/m^2) plotted against distance upstream (km).

The same data are illustrated in Figure 5. Note that 10 orders have been added to the list to accommodate the different distribution of orders found in the North Sydenham than in the St. Clair River (Harris 1999). Note also that the use of geometric means instead of arithmetic means changes slightly the shape of the curve for the St. Clair downstream reach compared to that shown previously (Harris 1999).

In view of the studies of unionid populations in the Sydenham (Clarke 1992; Mackie 1988; VanDerWal 2001*), it is worth mentioning that in the grab sampling used in both the North Sydenham and St. Clair Rivers, no live unionid specimens were found; only one or two empty shells. All live Bivalvia found in the North Sydenham were Sphaeriidae although a few empty shells of Dreisseniidae were recovered at the sampling site farthest downstream (site 18). Both Sphaeriidae and Dreisseniidae were found in the St. Clair River (Harris 1999).

In general terms, the results of the comparison of the North Sydenham River with the downstream reach of the St. Clair River fit with the "River Continuum Concept" proposed by Vannote et al. (1980) and later elaborated by Minshall et al (1985). As would be expected, the more lentic environment of the North Sydenham supports fewer of the predator orders and more shredders. However, the heavy sediment load in the North Sydenham and the absence of a steady flow and vigorous wave action are complicating factors. A comparable study of a third order stream in a gravel bed and fed by glacial melt water carrying a heavy sediment load would be expected to support a population of invertebrates more similar to that in the downstream reach of the St. Clair River.

Documents Cited (marked *)

Chambers, Brian. 1997. Private communication documenting water quality data for the North Sydenham River in the period 1983-1994 gathered by the Ontario Ministry of the Environment, London, Ontario. 108 pages.

Frais, W. 2002. Private communication documenting suspended solids for the service water intake at the Bayer/Nova plant downstream of Sarnia on the St. Clair River. 5 pages.

International Joint Commission. 1987. Great Lakes Water Quality Agreement of 1978 (amended 1987). 84 pages. [100 Ouellette Avenue, Windsor, Ontario, N9A 6T3.]

TABLE 5. Relative abundance of individuals in invertebrate orders in the North Sydenham River system (1996-2000) and the downstream reach of the St. Clair River (1990-1995) (Harris 1999).

Organism	North Sydenham River (all sites)		St. Clair River (downstream reach)	
	Mean log density	Geom. mean density*	Mean log density	Geom. mean density*
Diptera ++	2.579	379	3.194	1565
Oligochaeta	2.520	331	2.896	787
Gastropoda	0.581	4	2.475	298
Ephemeroptera ++	1.708	51	2.167	147
Bivalvia ++	1.201	16	1.818	66
Trichoptera ++	0.639	4	1.672	47
Hydracarina	0.210	2	1.454	28
Amphipoda ++	0.652	4	1.140	14
Nematoda	0.434	3	0.877	8
Cladocera	0.057	1	0.573	4
Turbellaria	0.245	2	0.438	3
Coleoptera	1.867	74	0.413	3
Ostracoda	0.014	1	0.295	2
Isopoda	0.163	2	0.138	1
Hemiptera	0.710	5	0.124	1
Lepidoptera	0.014	1	0.124	1
Megaloptera	0.492	3	0.069	1
Hydroida	0.032	1	0.055	1
Odonata	0.215	2	0.055	1
Decapoda	0.166	2	0.000	0
Hirudinea	0.134	1	0.000	0

* individual organisms/m^2

++ difference in geometric means is statistically significant at the 95% level of confidence; others are either not significant or are indeterminate because variances are significantly different

Kuley, E., and **W. R. Brooks**. 2001. Water Quality Assessment Program 2000 Annual Report. Prepared for the Sarnia-Lambton Environmental Association by Canadian ORTECH Environmental.

McDougall, Brian. 1998. Private communication documenting water flow data for 1993-1996 gathered by the St. Clair Region Conservation Authority, Strathroy, Ontario. 140 pages.

VanDerWal, J. J. 2001. The effect of turbidity on the freshwater mussels of the Sydenham River watershed, Ontario. MSc thesis, University of Western Ontario. 76 pages.

Jacques Whitford Environment Ltd. 2001. Report on the North Sydenham Recovery Project: synthesis and analysis of background data. 53 pages. (St. Clair Region Conservation Authority, Strathroy, Ontario).

Literature Cited

Clarke, A. H. 1992. Ontario's Sydenham River, an important refugium for native freshwater mussels against competition from the zebra mussel *Dreissena polymorpha*. Malacology Data Net, Volume 3, Numbers 1-4, 43-58.

Draper, N. R., and **H. Smith**. 1991. Applied Regression Analysis. John Wiley and Sons, New York, N. Y. 736 pages.

Dudley, T., and **N. H. Anderson**. 1982. A survey of invertebrates associated with wood debris in aquatic habitats. Melandria 39: 1-21.

Harris, I. W. E. 1999. Some factors affecting the density and richness of invertebrate populations in the near-shore sediments of the St. Clair River, 1990-1995. The Canadian Field-Naturalist 113(4): 576-584.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto, Ontario. 555 pages.

Mackie, G. L., and **J. M. Topping**. 1988. Historical changes in the unionid fauna of the Sydenham River watershed and downstream changes in shell morphometrics of three common species. Canadian Field-Naturalist 102: 617-626.

Merritt, R. W., and **K. W. Cummins**. 1988. An introduction to the aquatic insects of North America (2nd edition). Kendall/Hunt Publishing Co., Dubuque, Iowa. 722 pages.

Meyer, J. L. 1990. A blackwater perspective on riverine ecosystems. Bioscience 9: 643-651.

Minshall, G. W., K. W. Cummins, R. C. Petersen, C. E. Cushing, D. A. Bruns, J. R. Sedell, and **R. L. Vannote**. 1985. Developments in stream ecosystem theory. Canadian Journal of Fisheries and Aquatic Science 42: 1045-1055.

Pekarsky, B. L., P. R. Frassinet, M. A. Penton, and **D. J. Conklin, Jr.** 1990. Freshwater macroinvertebrates of northeastern North America. Cornell University Press, Ithaca, New York. 442 pages.

Pennak, R. 1989. Freshwater invertebrates of the United States (3rd edition). John Wiley and Sons, Toronto. 628 pages.

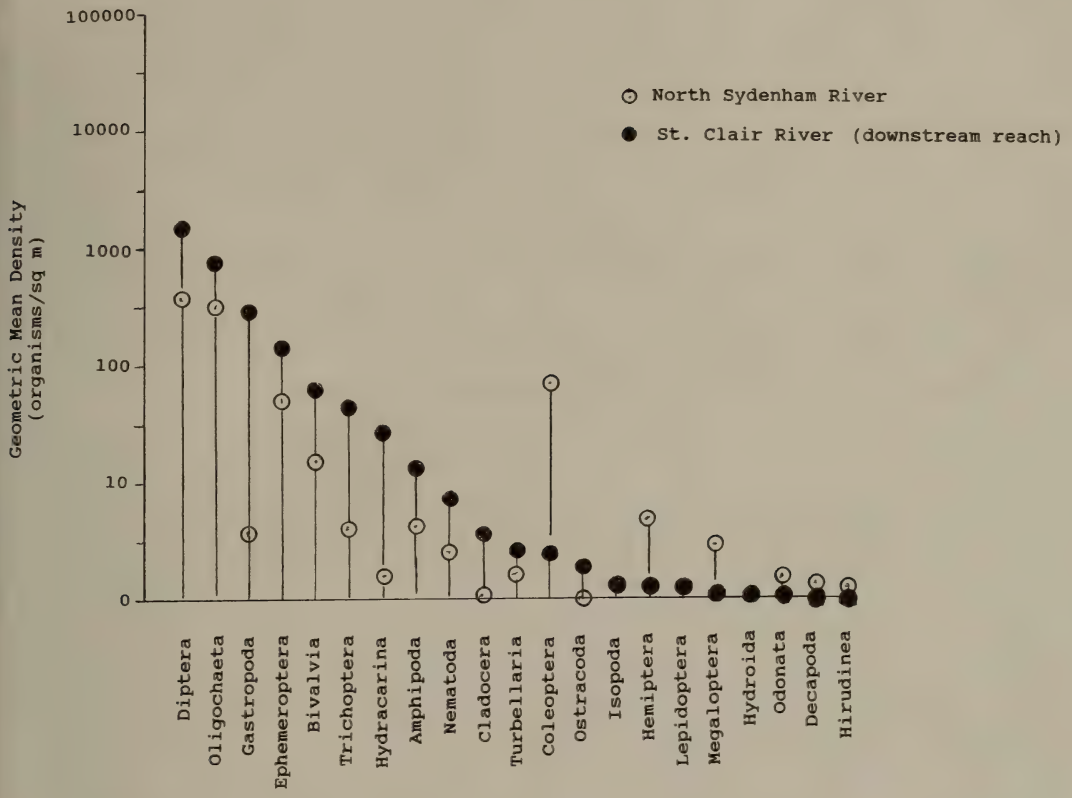


FIGURE 5. Relative abundance of invertebrate orders in the North Sydenham River (all sites combined) compared to the abundance of the same orders in the downstream reach of the St. Clair River (all sites combined).

Statzner, B., and **B. Higler**. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biology 16: 127-139.

Thorp, J. H., and **A. P. Covich**. 1991. Ecology and classification of North American freshwater invertebrates. Academic Press Inc., Toronto. 911 pages.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and **C. E. Cushing**. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science 37: 130-137.

Ward, J. V. 1986. Altitudinal zonation in a rocky mountain stream. Archiv fur Hydrobiologie, Supplement 74: 133-199.

Waters, T. F. 1972. The drift of stream insects. Annual Review of Entomology 17: 253-272.

Williams, D. D. 1981. Migrations and distribution of stream benthos. Perspectives in running water ecology. Plenum, New York. 430 pages.

Received 23 June 2002
Accepted 20 November 2003

New Records of Vascular Plants in the Yukon Territory V

WILLIAM J. CODY[1], CATHERINE E. KENNEDY[2], BRUCE BENNETT[2], and JENNIFER STANIFORTH[2].

[1] National Program on Environmental Health, Agriculture and Agri-Food Canada, Research Branch, Central Experimental Farm, Ottawa, Ontario K1A 0C6 Canada
[2] Department of Environment, Government of Yukon, Box 2703, Whitehorse, Yukon Y1A 2C6 Canada

William J. Cody, Catherine E. Kennedy, Bruce Bennett, and Jennifer Staniforth. 2003. New records of vascular plants in the Yukon Territory V. Canadian Field-Naturalist 117(2): 278-301.

Based on field reconnaissance in 2000 and 2001 throughout Yukon but particularly in the areas of the Upper Bonnet Plume River, Wind River, Eagle Plains and Vuntut National Park, information is provided on geographically significant plant occurrences. Three native taxa, *Draba kananaskis, Hieracium albiflorum* and *Prunella vulgaris* ssp. *lanceolata* and five introduced taxa, *Alopecurus geniculatus, Dactylis glomerata, Elymus junceus, Lotus corniculatus,* and *Verbena hastata* are reported new to the known flora of the Yukon Territory. Signifigant range extensions for 190 native and 24 introduced taxa are included. *Maianthemum dilatatum* is excluded from the Yukon flora.

Key Words: Vascular plants, Yukon Territory, flora, new records, range extensions, phytogeography.

Since the writing of *New Records of Vascular Plants in the Yukon Territory IV* (Cody et al. 2002), a considerable number of plant specimens have been submitted to Cody for identification and confirmation. The major submissions include the following locations and collectors: (1) Vuntut National Park by Bruce Bennett in connection with habitat inventories done for the National Park Service; (2) Lands adjacent to the Wind River by Bruce Bennett partially funded by the Canadian Parks and Wilderness Society; (3) Lands adjacent to the Upper Bonnet Plume River near the border of the Northwest Territories by Jennifer Staniforth while documenting vegetation for Yukon Renewable Resources Department; (4) Southern part of the Yukon Territory by Rhonda Rosie for the Yukon Territory Government Parks Branch; (5) Peel River Plateau and Richardson Mountains by Rhonda Rosie with support from the Canadian Parks and Wilderness Society; (6) Richardson Mountains by Greg Brunner during a vegetation analysis required by the Canadian Parks and Wilderness Society; (7) Kluane National Park area by Phil Caswell for the National Park Service as part of ongoing botanical inventories; (8) Southern Yukon at several former mine sites by Stu Withers in connection with reclamation of vegetation and soil stabilization; (9) Trout Lake area in Ivavik National Park by Jennifer Line while undertaking taxonomic studies of *Tofieldia*.

This paper serves to further update the *Flora of the Yukon Territory* (Cody 1996) and *Flora of the Yukon Territory, Second Edition* (Cody 2000) along with other records recently published (Cody et al. 1998, 2000, 2001, 2002). The floristic information presented earlier and updated here is essential for biological research and ongoing work relating to agriculture, forestry, sustainable resource management and wildlife management. With additions of three native and five introduced species reported here the flora now includes 1171 species. The new native species are all rare (as defined by Douglas et al. 1981). For convenience in this paper the Herbarium of the Yukon Department of Environment (formerly Yukon Department of Renewable Resources) has been given the acronym YUKH.

The taxa addressed in the body of this paper appear first in a synoptic list by Yukon status in alphabetical order. The taxa are then discussed in taxonomic order, as presented in the *Flora of the Yukon Territory* with citation of specimens and other pertinent information. Common names follow Cody (1996) and Douglas et al. (1984-2001).

Synoptic list by Yukon Status

Native taxa new to the Yukon Territory (3)

Draba kananaskis
Hieracium albiflorum
Prunella vulgaris ssp. *lanceolata*

Introduced taxa new to the Yukon Territory (5)

Alopecurus geniculatus
Dactylis glomerata
Elymus junceus
Lotus corniculatus
Verbena hastata

Range Extensions of Native Taxa within the Yukon Territory (190)

Aconitum delphinifolium ssp. *paradoxum*
Adoxa moschatellina
Agrostis exarata
Agrostis mertensii ssp. *mertensii*
Agrostis scabra var. *geminata*
Alnus crispa ssp. *crispa*
Alnus incana ssp. *tenuifolia*
Andromeda polifolia
Anemone multifida
Antennaria rosea ssp. *confinis*
Aquilegia formosa
Arabis boivinii
Arabis codyi

Arabis holboellii var. *retrofracta*
Arabis kamtschatica
Arnica angustifolia ssp. *attenuata*
Arnica chamissonis ssp. *chamissonis*
Arnica griscomii ssp. *frigida*
Artemisia dracunculus
Aster modestus
Astragalus bodinii
Astragalus tenellus
Betula neoalaskana
Betula occidentalis
Betula papyrifera
Bidens cernua
Calamagrostis canadensis ssp. *canadensis*
Calamagrostis canadensis ssp. *langsdorfii*
Calamagrostis purpurascens var. *purpurascens*
Calamagrostis stricta ssp. *inexpansa*
Cardamine umbellata
Carex arcta
Carex atherodes
Carex atrofusca
Carex bicolor
Carex bonanzensis
Carex brunnescens
Carex buxbaumii
Carex capillaris ssp. *capillaris*
Carex concinna
Carex deflexa
Carex eleusinoides
Carex flava
Carex franklinii
Carex garberi ssp. *bifaria*
Carex glacialis
Carex magellanica ssp. *irrigua*
Carex media
Carex microglochin
Carex obtusata
Carex pachystachya
Carex phaeocephala
Carex rostrata
Carex viridula
Carex williamsii
Castilleja pallida var. *caudata*
Cerastium arvense
Ceratophyllum demersum
Chrysanthemum integrifolium
Cicuta maculata var. *angustifolia*
Cinna latifolia
Circaea alpina ssp. *alpina*
Comandra umbellata ssp. *pallida*
Cystopteris fragilis
Cystopteris montana
Delphinium glaucum
Descurainia sophioides
Draba albertina
Draba borealis
Draba cana
Draba cinerea
Draba incerta
Draba macounii
Draba porsildii
Draba scotteri
Dryas crenulata
Dryas hookeriana
Dryopteris expansa
×*Elyhordeum macounii*
Elymus glaucus
Elymus macrourus
Elymus trachycaulus ssp. *andinus*
Elymus trachycaulus ssp. *glaucus*
Elymus trachycaulus ssp. *novae-angliae*
Elymus trachycaulus ssp. *subsecundus*
Elymus trachycaulus ssp. *trachycaulus*
Elymus trachycaulus ssp. *violaceus*
Epilobium hornemannii
Epilobium palustre
Equisetum variegatum ssp. *variegatum*
Eriophorum brachyantherum
Eriophorum callitrix
Eriophorum scheuchzeri
Eritrichium splendens
Erysimum cheiranthoides
Festuca lenensis
Festuca richardsonii
Festuca rubra
Fragaria virginiana ssp. *glauca*
Galium trifidum
Gymnocarpium dryopteris ssp. *dryopteris*
Hedysarum boreale ssp. *mackenzii*
Hierochloe alpina ssp. *alpina*
Iris setosa ssp. *interior*
Juncus balticus var. *littoralis*
Juncus triglumis ssp. *albescens*
Kalmia polifolia
Kobresia simpliciuscula
Lappula occidentalis
Leptarrhena pyrolifolia
Lesquerella arctica ssp. *arctica*
Lesquerella calderi
Lloydia serotina
Lycopodium alpinum
Lycopodium clavatum var. *monostachyon*
Lycopodium complanatum
Menyanthes trifoliata
Mimulus guttatus
Minuartia dawsonensis
Minuartia elegans
Minuartia obtusiloba
Minuartia yukonensis
Orobanche fasciculata
Osmorhiza depauperata
Oxytropis campestris ssp. *roaldii*
Oxytropis nigrescens ssp. *nigrescens*
Parnassia fimbriata
Pedicularis lanata
Phalaris arundinacea
Phlox hoodii
Pinus contorta ssp. *latifolia*
Poa leptocoma
Poa porsildii
Poa pratensis ssp. *alpigena*
Poa secunda ssp. *secunda*
Polemonium acutiflorum
Potamogeton filiformis var. *borealis*
Potamogeton vaginatus
Potentilla nivea
Primula egaliksensis
Puccinellia deschampsioides

Puccinellia nuttalliana
Pyrola minor
Ranunculus aquatilis var. *eradicatus*
Ranunculus eschscholtzii
Ranunculus flammula
Ranunculus pedatifidus ssp. *affinis*
Rosa woodsii
Rubus pedatus
Rubus pubescens
Rumex acetosa ssp. *alpestris*
Salix alaxensis ssp. *longistylis*
Salix arbusculoides
Salix arctica
Salix arctophila
Salix commutata
Salix fuscescens
Salix hastata
Salix niphoclada
Salix polaris
Salix pseudomonticola
Salix richardsonii
Salix rotundifolia ssp. *rotundifolia*
Sanguisorba canadensis ssp. *latifolia*
Schizachne purpurascens
Scirpus caespitosus ssp. *austriacus*
Senecio indecorus
Senecio sheldonensis
Senecio streptanthifolius
Senecio tundricola
Sibbaldia procumbens
Silene acaulis ssp. *acaulis*
Silene involucrata ssp. *involucrata*
Silene taimyrensis
Solidago canadensis var. *salebrosa*
Solidago multiradiata
Sparganium minimum
Stellaria borealis
Stellaria longifolia
Stipa comata
Streptopus amplexifolius ssp. *americanus*
Subularia aquatica ssp. *americana*
Taraxacum lyratum
Thalictrum alpinum
Thalictrum sparsiflorum ssp. *richardsonii*
Utricularia minor
Veratrum viride ssp. *eschscholtzii*
Viola epipsila ssp. *repens*
Viola langsdorfii
Viola nephrophylla

Range Extensions of Introduced Taxa within the Yukon Territory (24)

Agropyron pectiniforme
Agropyron sibiricum
Agrostis gigantea
Astragalus cicer
Bromus carinatus
Elymus elongatus ssp. *ponticus*
Elymus hispidus
Festuca trachyphylla
Lepidium sativum
Linaria vulgaris
Matricaria perforata
Onobrychis viciifolia
Phleum pratense
Plantago major
Poa compressa
Poa trivialis
Polygonum achoreum
Polygonum aviculare
Puccinellia distans
Senecio vulgaris
Sonchus asper
Spergularia rubra
Stellaria media
Trifolium pratense

Comments on a Taxon excluded from the Yukon Territory (1)

Maianthemum dilatatum

LYCOPODIACEAE

Lycopodium alpinum L., Alpine Club-moss – YUKON: undulating alpine midslope, Upper Bonnet Plume River Drainage, Site #120, 64°24'45"N 132°07'1"W, *J. Staniforth 00-078*, 4-12 July 2000 (DAO); strongly mounded-graminoid/moss/lichen pediment with frost boils, Upper Bonnet Plume River Drainage Site #131, 64°31'19"N 132°51'39"W, *J. Staniforth 00-092*, 4-12 July 2000 (DAO).

The specimens cited above are an extension of the known range in the Territory of about 175 kilometers east of a site mapped by Cody (1996) west of longitude 135°W.

Lycopodium clavatum L. var. *monostachyon* Hook. & Grev., Common Club-moss – YUKON: low damp area beside the water, WNW end of Trout Lake, 68°49'27"N 138°45'8"W, *J. M. Line 2000-81*, 28 July 2000 (DAO).

The specimen cited above is the northernmost yet found in the Territory. It is an extension of about 60 kilometers north of a site mapped by Cody (1996).

Lycopodium complanatum L., Flatbranch Club-moss – YUKON: Eagle Plains, 66°16'06"N 138°24'52"W, *G. Brunner 34b-00*, 21 July 2000 (DAO); undulating lower slope, shrub thicket with pockets of lichen, Upper Bonnet Plume River Drainage Site #111, 64°22'10"N 132°19'49"W, *J. Staniforth 00-056*, 6 July 2000 (DAO).

The first specimen cited above is an extension of the known range about 100 kilometers west of a site mapped by Cody (1996) west of longitude 138°W. The second specimen is an extension of the known range in the Territory of about 120 kilometers north of a site between longitudes 131°W and 132°W.

EQUISETACEAE

Equisetum variegatum Schleich. ssp. *variegatum*, Variegated Horsetail – YUKON: undulating riparian willow zone, Upper Bonnet Plume River Drainage Site #115, 64°25'03"N 132°22'56"W, *J. Staniforth 00-062*, 7 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody et al. 2001) of about 75 kilometers southeast of a site adjacent to the Snake River.

ASPIDIACEAE

Cystopteris fragilis (L.) Bernh., Fragile Fern – YUKON: undulating dry hummocky tundra alpine slope, Upper

Bonnet Plume Drainage Site #116, 64°24'28.7"N 132°07'54"W, *J. Staniforth 00-086*, 7 July 2000, (DAO).

The specimen cited above is an extension of the known range in the Territory of about 140 kilometers to the northeast of a site east of Mayo mapped by Cody (1996).

Cystopteris montana (Lam.) Bernh., Mountain Bladder Fern – YUKON: undulating spruce/shrub/lowshrub/forb/moss, Upper Bonnet Plume River Drainage Site #105, 64°26'6"N 132°15'28"W, *J. Staniforth 00-016*, 5 July 2000 (DAO); white spruce/willows, Richardson Mountains, 66°39'41"N 135°42'20"W, *G. Brunner 11-00*, 14 July 2000 (DAO).

The first specimen cited above is an extension of the known range in the Territory of about 240 kilometers northeast of a site west of Mayo mapped by Cody (1996). The second specimen cited above which is the northernmost yet found in the Territory is about 125 kilometers north of a site adjacent to the Wind River reported by Cody et al. (2002).

Dryopteris expansa (Presl) Fraser-Jenkins & Jermy, Northern Wood Fern – YUKON: alder/rose, Richardson Mts., 66°44'51"N 135°24'40"W, *G. Brunner 23-00*, 17 July 2000 (YUKH, Photo DAO).

The specimen cited above is an extension of the known range in the Territory of about 500 kilometers southwest from sites adjacent to the North Canol Road mapped by Cody (1996).

Gymnocarpium dryopteris (L.) Newm. ssp. *dryopteris*, Oak Fern – YUKON: in moist alpine meadow, Crescent Lake, 60°11'00"N 131°15'30"W, *R. Rosie 2103*, 22 July 2000 (DAO).

The specimen cited above is intermediate between sites mapped by Cody (1996) from the vicinity of Watson Lake and the South Canol Road.

PINACEAE

Pinus contorta Dougl. ex Loud. ssp. *latifolia* (Engelm.) Critchfield, Lodgepole Pine – YUKON: St. Elias Trail, Kluane National Park, 60°18'N 137°03'W, *P. Caswell 2000-Y-435*, 18 Aug. 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory of about 60 kilometers south of a site adjacent to the Alaska Hwy. just east of longitude 137°W reported by Cody et al. (2002).

SPARGANIACEAE

Sparganium minimum (Hartm.) Fries, Small Bur-reed – YUKON: submerged in shallow pond, Dog Creek Ponds, Vuntut National Park, 68°26'37"N 138°45'12"W, *B. Bennett 00-922*, 7 Aug. 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory of about 325 kilometers northwest of a site at Turner Lake reported by Cody et al. (2001).

POTAMOGETONACEAE

Potamogeton filiformis Pers. var. *borealis* (Raf.) St. John, Fine-leaved Pondweed – YUKON: submerged in shallow pond, Dog Creek Ponds, Vuntut National Park, 68°26'37"N 138°45'12"W, *B. Bennett 00-923*, 7 Aug. 2000 (DAO); plant fragments washed ashore, Trout Lake, 68°50'N 138°45'N, *J. M. Line 2000-139*, 28 July 2000 (DAO).

The specimens cited above are an extension of the known range in the Territory of about 100 kilometers northeast of sites just north of latitude 68°N reported by Cody et al. (1998).

Potamogeton vaginatus Turcz., Giant Pondweed – YUKON: submerged in shallow pond, Dog Creek Ponds, Vuntut National Park, 68°26'37"N 138°45'12"W, *B. Bennett 00-924*, 7 Aug. 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory of about 125 kilometers northwest of a site about 67°40'N mapped by Cody (1996).

POACEAE (GRAMINEAE)

Agropyron pectiniforme R. & S., Crested Wheat Grass – YUKON: gravel disturbed area, Alaska Highway at Destruction Bay, 61°15'07.6"N 138°48'19.8"W, *Cody & Cody 37070*, 25 July 2000 (DAO).

The nearest site of this introduced grass species known to Cody (1996) was in the vicinity of Haines Junction, about 90 kilometers to the southeast.

Agropyron sibiricum (Willd.) P.B., Siberian Wheatgrass – YUKON: waste ground along roadside, Ross River, 61°58'55.2"N 132°26'57.0"W, *Cody & Cody 36940*, 19 July 2000 (DAO).

This introduced species was only known to Cody (1996) from two localities: Whitehorse and Carmacks.

Agrostis exarata Trin., Spike Redtop – YUKON: in meadow along brook draining warm spring, McPherson Lake, 61°52'19"N 129°36'34"W, *R. Rosie 2090*, 6 Sept. 2000 (DAO).

Cody et al. (1998) extended the range of this rare species in the Territory (Douglas et al. 1981) to the vicinity of Frances Lake about 200 kilometers to the north of sites east of Watson Lake. The specimen cited above is a further extension to the north of about 30 kilometers.

Agrostis gigantea Roth, Creeping Bent Grass – YUKON: reclaimed mining waste dump, Brewery Creek Mine, 64°03.3'N 138°03.3'W, *S. Withers SW00-102*, 12 July 2000 (DAO); reclaimed area below leach pad, Brewery Creek Mine, 64°02.5'N 138°17.0'W, *S. Withers SW00-121*, 13 July 2000 (DAO).

The specimens cited above of this introduced species are from only the third known locality in the Territory. It was previously known only from the vicinities of Dawson and Carmacks.

Agrostis mertensii Trin. ssp. *mertensii*, Red Bent Grass – YUKON: dry upland bench with *Sibbaldia*, north of camp "Dandelion Site", Vuntut National Park, 68°29.14'N 138°50.35'W, *B. Bennett 00-1150*, 8 Aug. 2000 (DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996) and is an extension of the known range of about 125 kilometers to the northwest.

Agrostis scabra Willd. var. *geminata* (Trin.) Swallen – YUKON: reclaimed area near roadside, Sa Dena Hes Mine Site, 60°32.8'N 128°51.8'W, *S. Withers SW00-197*, 31 Aug. 2000 (DAO).

This variety was considered rare in the Territory by Douglas et al. (1981) where it was previously known from only five localities (Cody 1996; Cody et al. 1998).

Alopecurus geniculatus L., Water Meadow-foxtail (Figure 1) – YUKON: hidden in *Stelleria longifolia* clump, Horseshoe Slough Habitat Protection Area near Mayo, 63°26'N 135°06'W, *D. Mossop 8*, July 2000 (DAO).

This species which is introduced in Canada from Eurasia is new to the Territory (Cody 1996). It is common in SW British Columbia north to the Queen Charlotte Islands and rare in SE British Columbia. It can be separated from *A. alpinus* as follows:

A. Spikes oblong to short-cylindric; spikelets more than 3 mm long; glumes densely covered over the entire surface with long wooly hairs; lemma apices obtuse ..... *A. alpinus*

A. Spikes long-cylindric; spikelets 3.2 mm long or less; glumes with long hairs restricted to nerves and keel; lemma apices nearly truncate ..... *A. geniculatus*

Bromus carinatus Hook. & Arn., California Brome – YUKON: sandy silt riverbar with *Salix alaxensis* and *Taraxacum officinale* surrounding camp, La Biche River, 60°13.58'N 124°13.58'W, *B. Bennett 98-131*, 17 June 1998 (DAO).

Cody (1996) knew this introduced species in the Territory from a single site in the vicinity of Carcross. Cody et al. (1998) reported a second site from the vicinity of Watson Lake. The specimen cited above is an extension of the known range in the Territory of about 250 kilometers to the east of Watson Lake.

Calamagrostis canadensis (Michx.) Beauv. ssp. *canadensis*, Blue-joint – YUKON: lake edge, Sam Lake, Vuntut National park, 68°24'24"N 138°37'58"W, *B. Bennett 00-1144*, 5 Aug. 2000 (DAO).

This is the northernmost collection yet found in the Territory. The nearest site known to Cody (1996) was about 85 kilometers to the southeast.

Calamagrostis canadensis (Michx.) Beauv. ssp. *langsdorfii* (Link) Hultén – YUKON: Beaver River near Toobally, 60°33.362'N 126°11.959'W, *B. Bennett 98-692*, 14 Aug. 1998, (B. Bennett Herbarium, photo DAO); alpine meadow beside lake, Beavercrow Ridge, 60°13.38'N 124°34.834'W, *B. Bennett 98-688*, 17 Aug. 1998 (DAO).

The specimens cited above extend the known range in the Territory (Cody 1996) about 150 kilometers east of a site west of longitude 127°W.

Calamagrostis purpurascens R.Br. var. *purpurascens*, Purple Reedgrass – YUKON: subalpine, found with *Trisetum spicatum* and *Festuca baffinensis*, Kotaneelee Range, 60°14.31'N 124°07.19'W, *B. Bennett 98-708*, 19 June 1998 (DAO).

The specimen cited above is the easternmost yet found in the Territory (Cody 1996). It is an extension of about 80 kilometers east of a site adjacent to the Larsen Hotsprings reported by Cody et al. (2000).

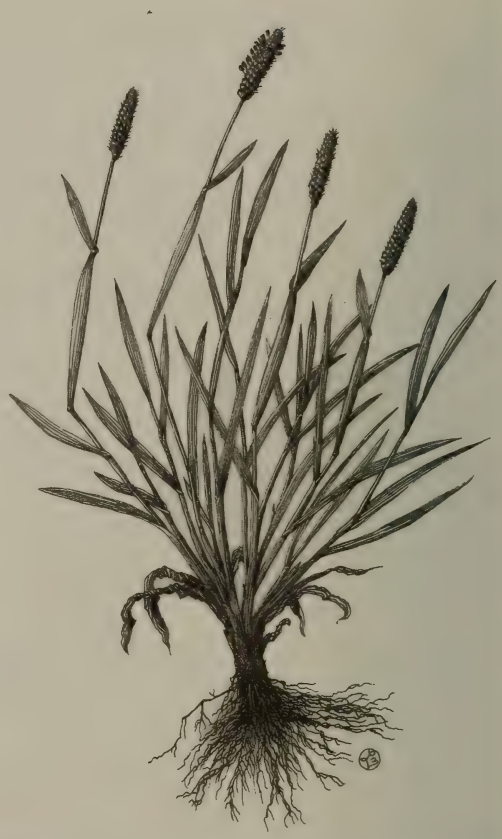


FIGURE 1. *Alopecurus geniculatus* L., Water Meadow-foxtail (drawn by Lee Mennell).

Calamagrostis stricta (Timm) Koeler ssp. *inexpansa* (Gray) C. W. Greene, Northern Reedgrass – YUKON: detachment slide, Richardson Mts., 66°52'N 135°50'W, *G. Brunner 22-00*, 17 July 2000, (DAO); loose sand near top of beach, Taco Bar, Peel River, 66°00'15"N 134°13'W, *B. Bennett 00-390*, 13 July 2000 (DAO); huge riverbar system, Peel River Camp #8, 65°56.03'N 134°58.84'W, *B. Bennett 00-774*, 9 July 2000 (DAO).

The specimens cited above extend the known distribution in the Territory about 150 kilometers to the southeast from a site north of the Dempster Hwy. known to Cody (1996).

Cinna latifolia (Trev.) Griseb., Nodding Wood-reed – YUKON: in meadow along brook draining warm spring, McPherson Lake, 61°52'19"N 129°36'34"W, *R. Rosie 2091*, 6 Sept. 2000 (DAO).

Cody et al. (1998) extended the known range of this rare species in the Territory (Douglas et al. 1981) to the vicinity of Frances Lake about 200 kilometers north of a site east of Watson Lake. The specimen cited above is a further extension to the north of about 30 kilometers.

Dactylis glomerata L., Orchard Grass (Figure 2) – YUKON: disturbed area near tailings dam, Sa Dena Hes Mine Site, 60°32.8'N 128°51.8'W, *S. Withers SW00-176*, 31 Aug. 2000 (B. Bennett Herbarium,

FIGURE 2. *Dactylis glomerata* L., Orchard Grass (drawn by Lee Mennell).

photo DAO); reclaimed area near roadside, Sa Dena Hes Mine Site, 60°32.8'N'128°51.8'W, *S. Withers SW00-198*, 31 Aug. 2000 (DAO).

The specimens cited above are the first records of this introduced species in the Territory. Cody (1996) suggested that it should be looked for in areas north of the British Columbia border.

×*Elyhordeum macounii* (Vasey) Barkworth & D. R. Dewey (×*Agrohordeum macounii* (Vasey) Lepage, *Elymus macounii* Vasey) – YUKON: only seen in one small patch near salt lake, Takhini Salt Flats, 60° 51.23'N 135°42.55'W, *B. Bennett 99-213*, 26 July 1999 (DAO) (determined by S. Darbyshire).

Porsild (1951) knew this hybrid from Hootalinqua on the Yukon River, Mayo and Mile 937 (ca Km 1558) on the Alaska Hwy. and in addition a specimen collected by Malte from Dawson was revised to *Agrohordeum macounii*. ×*Agrohordeum macounii* was reported as occurring in the Yukon Territory by Cody (1996).

Elymus elongatus (Host) Runemark ssp. *ponticus* (Podp.) Melderis, Tall Wheatgrass – YUKON: disturbed area near tailings dam, Sa Dena Hes Mining Site, 60°32.8'N 128°51.8'W, *S. Withers SW00-183*, 31 Aug. 2000 (DAO); reclaimed area near roadside, same locality, *S. Withers SW00-200*, 31 Aug. 2000 (DAO).

This introduced species was first reported from a site south of Carcross at the British Columbia border by Cody et al. (2002). It was presumably the result of planting seeds to reclaim eroding soil in the area cited above.

Elymus glaucus Buckl., Western Rye Grass – reclaimed mining waste dump, Brewery Creek Mine, 64°03.3'N 138°03.2'W, *S. Withers SW00-109*, 12 July 2000 (DAO).

This species was previously known in the Territory in the southwest (Cody 1996) and extreme southeast (Cody et al. 2000). It was undoubtedly introduced at the site listed above.

Elymus hispidus (Opiz) Meld. (*Agropyron intermedium* (Host) Beauv., *Elytrigia intermedia* (Host) Nevski), Intermediate Wheatgrass – YUKON: disturbed roadside, Robert Campbell Hwy., Km 467, 62°10.20'N 134°18'W, *B. Bennett 99-542*, 19 Aug. 1999 (DAO).

Cody et al. (1998) reported the first occurrence of this introduced Eurasian species in the Territory from a roadside adjacent to the La Biche River about 600 kilometers southeast of the introduction cited above. In addition a second specimen has since been collected in the southeast in a disturbed area beside the La Biche Airstrip, 60°07'42"N 124°02'21"W, *B. Bennett 98-581*, 21 June 1998 (DAO). These Bennett specimens were accidentally reported as *Elymus repens* by Cody et al. (2000).

Elymus junceus Fischer (*Psathyrostachys juncea* (Fischer) Nevski), Russian Wild Rye – YUKON: Kluane National Park, Haines Hwy. ca Km 195 at Dezadeash Lake Pull Out, 60°22'46.0"N 137°03'8.9"W, *P. Caswell s.n.*, 19 July 2000 (Kluane National Park Herbarium, photo DAO) (determined by S. Darbyshire).

This species, which is introduced from Asia, is new to the Yukon Territory. Elsewhere in North America it is known from the Prairie Provinces and south to Arizona.

Densely tufted perennial; culms 30-120 cm high, erect or decumbent at base; old sheath bases more or less persistent; leaf blades flat to involute, 1-5 mm wide, glabrous to scaberulous; spike 3-16 cm long, 5-17 mm wide, erect, the rachis at maturity disarticulating; spikelets 2(3) per node, 7-10(12) mm long (excluding awns), strongly overlapping; glumes subulate, (4)5-9 mm long, obscurely 1-nerved, acute to awn-tipped, distinctly shorter than the lowermost lemma; lemma lance-elliptical, 6-10 mm long, scabrous to densely short-hairy, tapered to a sharply acute tip or with an awn to about 3 mm long; anthers 2.5-5 mm long.

Elymus macrourus (Turcz.) Tzvelev, Thick-spike Wild Rye – YUKON: on gravel bar of Peel River, Peel River Plateau, 66°50'30"N 134°57'00"W, *R. Rosie 2147*, 17 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 60 kilometers east of a site adjacent to the Dempster Hwy.

Elymus trachycaulus (Link) Gould ex Shinners ssp. *trachycaulus*, Slender Wheatgrass – YUKON: common on riverbar, Wind River Camp #4, 65°22.89'N 135°26.1'W, *B. Bennett 00-370*, 5 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 200 kilometers north of a site in the vicinity of Mayo.

Elymus trachycaulus (Link) Gould ssp. *andinus* (Scribn. & Smith) A. & D. Löve – YUKON: riverbar in sand, Dog Creek Camp, Vuntut National Park, 68°27.53'N 138°44.47'W, *B. Bennett 00-1189*, 3 Aug. 2000 (DAO); large arctic ground squirrel mound on tundra, Dog Creek Ponds, Vuntut National Park, 68°26.37'N 138°45.12'W, *B. Bennett 00-1190*, 8 Aug. 2000 (DAO).

The specimens cited above are the northernmost yet found in the Territory (Cody 1996). The nearest known site is about 100 kilometers to the southwest.

Elymus trachycaulus (Link) Gould ex Shinners ssp. *glaucus* (Pease & Moore) Cody – YUKON: start of trail in John Connally RV Park, 62°13'51.29"N 133°21' 02.65"W, *B. Bennett 99-539*, 19 Aug. 1999 (DAO); loose sand near top of beach, Taco Bar, Peel River, 66°00.15'N 134°13'W, *B. Bennett 00-393*, 13 July 2000 (DAO).

The first specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 100 kilometers north of a site adjacent to the South Canol Road. The nearest site to the second specimen is about 250 kilometers to the northwest adjacent to the Porcupine River.

Elymus trachycaulus (Link) Gould ex Shinners ssp. *novae-angliae* (Scribn.) Tzvelev – YUKON: on gravel bar of Caribou River, 66°15'41"N 135°31'28"W, *R. Rosie 2149*, 15 July 2000 (DAO); on gravel bar of Peel River, Peel River Plateau, 66°50'30"N 134°57'W, *R. Rosie 2148*, 17 July 2000 (DAO) (determined by S. Darbyshire).

The specimens cited above are the northernmost yet found in the Territory (Cody 1996). They extend the known range about 290 kilometers northwest of a site adjacent to the Upper Bonnet Plume River.

Elymus trachycaulus (Link) Gould ex Shinners ssp. *subsecundus* (Link) Gould – YUKON: in crack of bedrock on exposed cliff, Wolf River/Nisutlin River confluence, 60°16.54'N 132°33.1'W, *B. Bennett 99-502*, 16 Aug. 1999 (DAO); under *Pinus contorta* in sand, Nisutlin River, end of old beach ridge, *B. Bennett 98-586*, 29 July 1998 (DAO).

The specimens cited above extend the known range in the Territory (Cody 1996) about 50 kilometers east of a site adjacent to Jake's Corner in the south.

Elymus trachycaulus (Link) Gould ex Shinners ssp. *violaceus* (Hornem.) A. & D. Löve – YUKON: riverbar, Wind River, 65°46.36'N 135°10.71'W, *B. Bennett 00-798*, 8 July 2000 (DAO) (determined by S. Darbyshire).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 75 kilometers to the southeast of a site north of latitude 66°N.

Festuca lenensis Drob., Tundra Fescue – YUKON: on dry stony mountain top, Richardson Mts., 66°38'N 135°51'W, *R. Rosie 2150*, 16 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Richardson Mts. (Cody 1996) of about 50 kilometers south from the Dempster Hwy. at the Northwest Territory boundary.

Festuca richardsonii Hook., Richardson's Fescue – YUKON: reclaimed area near roadside, Sa Dena Hes Mine Site, 60°32.8'N 128°51.8'W, *S. Withers SW00-194*, 31 Aug. 2000 (DAO); common on riverbar, Little Wind River/Wind River confluence, 65°22.89'N 135°26.1'W, *B. Bennett 00-373*, 5 July 2000 (DAO); riverbar near more established willows, Peel River Camp #8, 65°56.03'N 134°58.84'W, *B. Bennett 00-770*, 9 July 2000 (DAO).

The first specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 250 kilometers to the southeast from sites adjacent to the northern part of South Canol Road. The other two specimens are the first records of this species between latitudes 64°N and 66°N east of the Dempster Hwy.

Festuca rubra L. s.l., Red Fescue – YUKON: riverbar, Wind River Camp #6, 65°40.46'N 135°11.76'W, *B. Bennett 00-860*, 7 July 2000 (DAO); sandy gravel clearing, Top of the World Hwy., Km 23, 64°08' 05.0"N 139°44'27.0"W, *Cody & Cody 37035*, 22 July 2000 (DAO) (determined by S. Darbyshire).

Cody (1996) knew this species in the Territory only as far north as about latitude 64°30'N adjacent to the Dempster Hwy. The first specimen cited above is the northernmost yet found in the Territory and is an extension of the known range of about 140 kilometers east of sites adjacent to the Dempster Hwy. The second specimen is the first record from the Top of the World Hwy.

Festuca trachyphylla L., Hard Fescue – YUKON: reclaimed mining waste dump, Brewery Creek Mine, 64°03.3'N 138°03.2'W, *S. Withers SW00-112, SW00-116A*, 12 July 2000 (DAO); open roadside and reclaimed area near roadside, Sa Dena Hes Mine Site, 60°32.8'N 128°51.8'W, *S. Withers SW00-195, SW00-209*, 31 Aug. 2000 (DAO); seeded gravel slope, Campbell Hwy. Km 380, 62°03'34.2"N 132°52' 82.2"W, *Cody & Cody 37584*, 30 July 2001 (DAO).

Cody (1996) knew this introduced species only from the vicinity of Dawson. Cody et al. (2001) recorded a second site from adjacent to the Alaska Hwy. between Kluane Lake and the Alaska border. The first specimen cited above is from a site about 60 kilometers east of Dawson and the second site is from the southeast about 50 kilometers north of Watson Lake. The last site is from an area just northwest of Ross River.

Hierochloe alpina (Sw.) R. & S. ssp. *alpina*, Alpine Holy Grass – YUKON: talus slope near river, Deception Mountain, Wind River, 65°36.03'N 135°28.41'W, *B. Bennett 00-418*, 7 July 2000 (DAO).

The specimen cited above is the first known record from the Wind River area in the Territory (Cody 1996). It is however known from the Bonnet Plume River to the southwest and from north of the Peel River to the north.

Phalaris arundinacea L., Reed Canary Grass – YUKON: Quill Creek, Kluane National Park, 60°40'N 137°22'W, *P. Caswell 2000-Y-436*, 17 July 2000 (DAO).

This species was considered rare in the Territory by Douglas et al. (1981). The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 150 kilometers west of a site in the vicinity of Whitehorse.

Phleum pratense L., Timothy – YUKON: open roadside, Sa Dena Hes Mine Site, 60°32.8'N 128°51.8'W, *S. Withers SW00-232*, 31 Aug. 2000 (DAO).

Timothy is not a common introduction in southeastern Yukon. The specimen cited above is from a site about 90 kilometers northwest of a site east of Watson Lake.

Poa compressa L., Canada Bluegrass – YUKON: open roadside, Sa Dena Hes Mine Site, 60°32.8'N 128° 51.8'W, *S. Withers SW00-223*, 1 Sept. 2000 (DAO).

This is not a common introduction in the Yukon. Cody (1996) knew it only from the vicinity of Whitehorse and the South Canol Road. The specimen cited above is from about 225 kilometers east of the Canol Road.

Poa leptocoma Trin., Bog Bluegrass – YUKON: exposed alpine ridge, north slope of Golden Horn Mountain, 60°34.2'N 135°03.2'W, *S. Withers SW00-170*, 24 Aug. 2000 (DAO).

This is a widely scattered species throughout the Territory (Cody 1996). The specimen cited above is from about 200 kilometers east of a site near the south end of Kluane Lake.

Poa porsildii Gjaerevoll – YUKON: undulating upper slope, moist hummocky tundra, Upper Bonnet Plume River Drainage Site #108, 64°28'05"N 132°04'15"W, *J. Staniforth 00-039*, 5 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 135 kilometers to the northeast and about 175 kilometers from the east end of North Canol road to the southeast.

Poa pratensis L. ssp. *alpigena* (Blytt) Hiit. – YUKON: open meadow near outfitter's camp, Wind River, McClusky Lake, 64°34.19'N 134°25.77'W, *B. Bennett 00-243*, 2 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 125 kilometers northeast of a site in the vicinity of Mayo.

Poa secunda Presl ssp. *secunda*, Sandberg Bluegrass – YUKON: riverbank, 4' above river, silty sand with cobbles, La Biche River, 60°04.22'N 124°03.09'W, *B. Bennett 95-165*, 12 June 1995 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 200 kilometers east of a site adjacent to the Coal River Springs (Cody et al. 2000).

Poa trivialis L., Rough Bluegrass – YUKON: open roadside, southwest facing 15 degree slope, Sa Dena Hes Mine Site, 60°32.8'N 128°51.8'W, *S. Withers SW00-212*, 1 Sept. 2000 (DAO).

The specimen cited above is an extension of the known range of this introduced species in the Territory (Cody 1996) of about 240 kilometers east of a site adjacent to the Canol Road.

Puccinellia deschampsioides Th. Sor., Polar Alkali Grass – YUKON: on disturbed gravel near float plane landing, Johnson Lake, Faro, 62°12.23'N 133°23. 112'W, *B. Bennett 99-551*, 19 Aug. 1999 (DAO).

Douglas et al. (1981) considered this species rare in the Territory. The specimen cited above is an extension of about 175 kilometers southeast of a site adjacent to Pelly Crossing mapped by Cody (1996).

Puccinellia distans (Jacq.) Parl., Spreading Alkali Grass – YUKON: sporadic in patches near fence, Takhini Salt Flats, 60°51.23'N 135°42.55'W, *B. Bennett 99-224*, 26 July 1999 (DAO) (determined by S. Darbyshire); roadside gravel, Tagish Campground, 60°18'58.2"N 134°15'17.9"W, *Cody & Cody 36924*, 18 July 2000 (DAO); gravel area by closed restaurant, Robert Campbell Hwy., Km 467.5, 62°11'58.4'N 134°22'14.4"W, E of Drury Creek, *Cody & Cody 36984*, 20 July 2000 (DAO); roadside gravel pit, Campbell Hwy., Km 386, 61°59'25.8"N 132°26'14"W, *Cody & Cody 36985*, 20 July 2000 (DAO) (determined by L. Consaul).

Cody (1996) considered this introduced species rare in the Territory. The first specimen cited above is an extension of about 100 kilometers east of a site northwest of Haines Junction. The second and third specimens extend the known range southeast of Whitehorse and along the Campbell Hwy. to near Ross River.

Puccinellia nuttalliana (Schult.) Hitchc., Nuttall's Alkali Grass – YUKON: gravel cleared area, Faro, 62°13'59.2"N 133°20'57.8"W, *Cody & Cody 36968*, 19 July 2000 (DAO) (determined by L. Consaul).

The specimen cited above is an extension of the known range in the Territory of about 110 kilometers southeast of a site northeast of Carmacks mapped by Cody (1996).

Schizachne purpurascens (Torr.) Swallen, False Melic – YUKON: on steep dry west-facing slope in valley, Crescent Lake, 60°11'00"N 131°09'30"W, *R. Rosie 2117*, 22 July 2000 (DAO).

Although this species is widespread in distribution, it is rare in the Yukon Territory where it is known only in the southeast (Cody 1996; Cody et al. 1998). The specimen cited above is intermediate between sites west of 127°W and 133°W.

Stipa comata Trin. & Rupr., Needle-and-Thread – YUKON: south-facing slope in sandy well drained soil, Canyon Creek draining Aishihik Lake, 60°51.31'N 137°04.15'W, *B. Bennett 01-002*, 21 April 2001 (DAO).

Cody (1996) knew this species in the Territory from only four locations between Whitehorse and just north of the Pelly River. The specimen cited above is from a site about 75 kilometers southwest of the nearest site known to Cody.

CYPERACEAE

Carex arcta Boott, Northern Clustered Sedge – YUKON: in moist meadows in valley near Rudy Lakes, 60°13'00"N 131°12'30"W, *R. Rosie 2111*, 23 July 2000 (DAO).

This species was considered rare in the Territory by Douglas et al. (1981). The specimen cited above is from a site about 60 kilometers east of a site east of Teslin.

Carex atherodes Spreng., Awned Sedge – YUKON: red rock seep near confluence with Peel River, Wind River, 65°50'N 135°18'W, *B. Bennett 00-451*, 8 July 2000 (DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). It is from a site about 280 kilometers northeast of Dawson.

Carex atrofusca Schk., Dark-brown Sedge – YUKON: undulating lower slope, *Dryas* outwash floodplain, Upper Bonnet Plume River Drainage, 64°32'10"N 132°19'40"W, *J. Staniforth 00-052*, 6 July 2000 (DAO); muddy slough on riverbar, Wind River, 65°12.49'N 135°13.17'W, *B. Bennett 00-455*, 5 July 2000 (DAO).

Cody et al. (2000) reported a collection from the headwaters of the Bonnet Plume River about 45 kilometers east of the specimen cited above. These are only the second and third known sites between latitudes 64°N and 66°N east of the Dempster Hwy.

Carex bicolor All., Two-coloured Sedge – YUKON: wet creek bank with *Equisetum*, upper Sheep Creek, 61°34.5'N 133°02.4'W, *S. Withers SW00-022A*, 2 July 2000 (B. Bennett Herbarium, photo DAO).

This is a rare widely scattered species in the Territory (Cody 1996). The nearest site to that listed above is in the vicinity of Frances Lake, about 230 kilometers to the east.

Carex bonanzensis Britt., Yukon Sedge – YUKON: wetland, Richardson Mts., 66°11'04"N 136°25'W, *G. Brunner 31-00*, 18 July 2000 (DAO).

The specimen cited above is intermediate between sites mapped by Cody (1996) from about 275 kilometers southwest adjacent to the Dempster Hwy. and from about 200 kilometers northwest adjacent to the Porcupine River.

Carex brunnescens Poir., Brownish Sedge – YUKON: Auriol Trail, Kluane National Park, 60°42'N 137°27'W, *P. Caswell PPC-2000-Y-300*, 10 Aug. 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 200 kilometers to the west from a site adjacent to Jake's Corner.

Carex buxbaumii Wahlenb., Buxbaum's Sedge – YUKON: wet sedge meadow, north shore of Caribou Lake, 60°31.9'N 134°16.9'W, *S. Withers SW00-141*, 29 July 2000 (DAO); "Cranberry Lake", Kluane National Park, 60°16'40"N 137°37'30"W, *R. D. Wickstrom s.n.*, 14 Aug. 1974 (DAO).

Cody (1996) knew this species in the Territory only from six localities, all south of latitude 62°N. Since that time Cody et al. (1998, 2000) have added sites at Frances Lake and the Nisutlin River Delta. The first specimen cited above is intermediate between the Nisutlin River Delta and Whitehorse and the second specimen is an extension of the known range of about 130 kilometers south from the vicinity of Kluane Lake.

Carex capillaris L. ssp. *capillaris*, Hairlike Sedge – YUKON: open meadow near outfitter's camp, McClusky Lake, Wind River, 64°34.19'N 134°25.77'W, *B. Bennett 00-286*, 2 July 2000 (DAO); amongst *Salix* and *Parnassia* at edge of river in camp, same locality, *B. Bennett 00-338*, 2 July 2000 (DAO); riverbar at base of cliff, Wind River, 65°12.49'N 135°13.17'W, *B. Bennett 00-369*, 5 July 2000 (DAO); moist draw near creekside in gravelly soil, Wind River Camp #6, 65°40.46'N 135°11.76'W, *B. Bennett 00-845*, 7 July 2000 (DAO).

The specimens cited above are new to the area between latitudes 64° and 66°N east of the Hart River.

Carex concinna R.Br., Low Northern Sedge – YUKON: moist meadow under *Salix alaxensis*, Dog Creek Camp, Vuntut National Park, 68°27'53"N 138°44'47"W, *B. Bennett 00-1033*, 3 Aug. 2000 (DAO).

The specimen cited above is only the second known to Cody (1996) from north of 68°N.

Carex deflexa Hornem., Bent Sedge – YUKON: Eagle Plains, 66°33'N 136°48'W, *L. Schroeder 15*, 24 July 1994 (DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). It is an extension of about 60 kilometers north of a site just north of latitude 66°N.

Carex eleusinoides Turcz., Goosegrass Sedge – YUKON: wet and waterlogged tussock tundra, Dog Creek Camp, Vuntut National Park, 68°27.53'N 138°44.47'W, *B. Bennett 00-1170*, 4 Aug. 2000 (DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). It is an extension of the known range of about 75 kilometers northwest of a site just south of latitude 68°N.

Carex flava L., Yellow Sedge – YUKON: along gravelly/sandy beach near warm spring, McPherson Lake, 61°52'19"N 129°36'34"W, *R. Rosie 2088*, 6 Sept. 2000 (DAO).

This species, which is rare in the Territory (Cody 1996) was previously known from a single locality about 80 kilometers east of Watson Lake. The specimen cited above is an extension of the known range of about 230 kilometers to the northwest.

Carex franklinii Boott, Franklin's Sedge – YUKON: riverbar, Wind River Outfitter's Camp, 64°34.43'N 134°28.88"W, *B. Bennett 00-476*, 2 July 2000 (DAO); Wind River Camp #1, 64°40.39'N 134°35.96'W, *B. Bennett 00-733*, 2 July 2000 (DAO); open dolomite delta in silty creek-bed, Wind River, 64°48.46'N 134°41.34'W, *B. Bennett 00-323* (B. Bennett Herbarium, photo DAO); steep solifluction slope, Dog Creek Camp, Vuntut National Park, 68°27.53'N 138°44.47'W, *B. Bennett 00-1065*, 7 Aug. 2000 (DAO).

The Wind River specimens cited above are an extension of the known range in the Territory (Cody 1996) of about 125 kilometers southeast of a site adjacent to the Hart River. The Dog Creek Camp specimen is an extension of the known range in the far north of about 75 kilometers from sites adjacent to the Firth River.

Carex garberi Fern. ssp. *bifaria* (Fern.) Hultén, Garber's Sedge – YUKON: silty mud on edge of lake, Wind River Camp #2, 64°51.83'N 134°38.85'W, *B. Bennett 00-828*, 4 July 2000 (DAO); silty seep on edge of river, Peel River, 65°58.06'N 134°49.69'W, *B. Bennett 00-431*, 10 July 2000 (DAO); silty hard packed river bank with *Parnassia palustris* under *Salix alaxensis*, Dog Creek Camp, Vuntut National Park, 68°27.

53'N 138°44.47'W, *B. Bennett 00-1037*, 4 Aug. 2000 (DAO).

Cody (1996) knew this sedge species only as far north as about 64°N in the vicinity of Dawson. The Wind and Peel river specimens cited above extend the known range in the Territory about 250 kilometers north of a site in the vicinity of Mayo. The Dog Creek specimen is an extension of the known range in the Territory of about 525 kilometers north of Dawson.

Carex glacialis Mack., Glacier Sedge – YUKON: on steep vegetated slope above river, Wind River Camp #1, 64°40.39'N 134°35.96'W, *B. Bennett 00-734*, 2 July 2000 (DAO); high alpine in loose talus, Wind River, 64°48.46'N 134°41.34'W, *B. Bennett 00-291*, 3 July 2000 (DAO); open dolomite delta, same locality, *B. Bennett 00-293*, 3 July 2000 (DAO); open slopes, moist areas, Wind River, Deception Mountain, 65°36.03'N 135°28.41'W, *B. Bennett 00-442* and *00-275*, 7 July 2000 (DAO); moderately steep south-facing slope, Bonnet Plume River, 64°37'32"N 133°17'20"W, *V. Loewen 99-32-97*, 15 July 1999 (DAO); alpine slope – *Dryas*/forb/sedge, Upper Bonnet Plume River Drainage Site #100, 64°20'20"N 132°15'28"W, *J. Staniforth 00-013*, 5 July 2000 (DAO); convex lower ridge – dry, well drained rocky slope, Upper Bonnet Plume River Drainage Site #132, 64°31'19"N 132°51'39"W, *J. Staniforth 00-039*, 7 July 2000 (DAO).

Between latitudes 64°N and 66°N Cody (1996) knew this species only as far east as about 66°04'N 135°50'W. The specimens cited above extend the known distribution about 50 kilometers to the northeast and about 200 kilometers to the southeast.

Carex magellanica Lam. ssp. *irrigua* (Wahlenb.) Hiit., Bog Sedge – YUKON: in basin bog in old oxbow on Eagle River, Eagle Plains, 66°16'N 136°31'W, *R. Rosie 2140, 2141*, 18 July 2000 (DAO).

Cody (1996) knew this species in the Territory north to about latitude 64°N. The specimens cited above extend the known distribution about 280 kilometers to the north.

Carex media R.Br., Alpine Sedge – YUKON: mucky bank of tributary stream in gravels, Wind River, 65° 46.36'N 135°10.71'W, *B. Bennett 00-129*, 8 July 2000 (DAO).

The specimen cited above is from the only site between latitudes 64°and 66°N east of the Dempster Hwy (Cody 1996).

Carex microglochin Wahlenb., Few-seeded Bog or Bristle Sedge – YUKON: in meadow near river amongst older *Picea glauca* forest with a little *Populus balsamifera*, Wind River Camp #1, 64°40.39'N 134°35.96'W, *B. Bennett 00-717*, 2 July 2000 (DAO); silty mud on edge of lake, Wind River Camp #2, 64°51.83'N 134°38.85'W, *B. Bennett 00-826*, 4 July 2000 (DAO).

The specimens cited above are the only known collections between latitudes 64°N and 66°N (Cody 1996) about 180 kilometers east of a site adjacent to the Dempster Hwy.

Carex obtusata Liljeb., Blunt Sedge – YUKON: severly mounded valley floor wetland in undulating valley floor sedge meadow, Upper Bonnet Plume River Drainage Site #142, 64°22'47"N 132°07'52"W, *J. Staniforth 00-127*, 4-12 July 2000 (DAO).

The specimen cited above is the only collection between latitudes 64° and 66° east of the Dempster Hwy. The nearest collection to the southwest, just west of longitude 135° is about 200 kilometers (Cody 1996).

Carex pachystachya Cham., Thick-headed Sedge – YUKON: St. Elias Trail, Kluane National Park, 60°18'N 137°03'W, *P. Caswell, PPC-2000-Y-310*, 18 Aug. 2000 (DAO); wet lakeshore inlet of Caribou Creek to Caribou Lake, 60°32.0'N 134°15.9'W, *S. Withers SW00-168*, 7 Aug. 2000 (DAO).

Cody (1996) knew this rare species in the Territory, southeast Kluane Park and just west of Watson Lake. The first collection cited above is from a site just northeast of the first Kluane Park collection and the second is intermediate between Watson Lake and Kluane Park.

Carex phaeocephala Piper, Dunhead Sedge – YUKON: in wetland south of Squanga Lake, 60°26.20'N 133° 35.24'W, *R. Rosie 2171*, 13 Aug. 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 190 kilometers east of a site adjacent to the Haines Hwy. just north of latitude 60°N.

Carex rostrata Stokes – YUKON: slough in creek near camp, Dog Creek Camp, Vuntut National Park, 68°27.52'N 138°44.47'W, *B. Bennett 00-1169*, 4 Aug. 2000 (DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). It is an extension of the known range of about 125 kilometers north from a site adjacent to the Porcupine River.

Carex viridula Michx., Green Sedge – YUKON: along sandy-gravelly shore of small lake in uplands, Squanga Lake, 60°27'N 133°38'W, *R. Rosie 2172*, 12 Aug. 2000 (DAO); among *Salix* at mouth of intermittent ephemeral creek, Nisutlin River Delta, 60°13'11"N 132°31'23"W, *B. Bennett 98-484*, 28 July 1998 (DAO).

This is a rare species in the Territory (Douglas et al. 1981). The specimens cited above are from sites intermediate between Whitehorse and Watson Lake.

Carex williamsii Britt., William's Sedge – YUKON: silty seep on edge of river, Peel River Site #1, 65°58.06'N 134°49.69'W, *B. Bennett 00-433*, 10 July 2000 (DAO).

This is a rare species in the Territory (Douglas et al. 1981). The specimen cited above is an extension of the known range in the Territory of about 225 kilometers northeast of sites adjacent to the Dempster Hwy.

Eriophorum brachyantherum Trautv., Short-anthered Cotton-grass – YUKON: in hummocky *Picea*/*Salix* forest near river, McClusky Lake, Wind River, 64°34.19'N 134°25.77'W, *B. Bennett 00-328*, 2 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory of about 80 kilometers northeast of a site north of Mayo (Cody 1996).

Eriophorum callitrix Cham., Arctic Cotton-grass – YUKON: steep solifluction slope in moist area, Dog Creek Camp, Vuntut National Park, 68°27.53'N 138°44.47'W, *B. Bennett 00-1071*, 2 Aug. 2000 (DAO).

Cody (1996) knew this species in the Territory west of longitude 135°W north to about 65°45'N and then disjunct to the Mt. Sedgwick area in the British Mountains. The specimen cited above is from a site about 40 kilometers southeast of Mt. Sedgewick.

Eriophorum scheuchzeri Hoppe, Scheuchzer's Cotton-grass – YUKON: boggy tussock tundra near small pond, Wind River Camp #2, 64°51.83'N 134°38.85'W, *B. Bennett 00-814*, 4 July 2000 (DAO); silty seep at edge of river, Peel River Site #1, 65°58.06'N 134°49.69'W, *B. Bennett 00-403*, 10 July 2000 (DAO); boggy area with open pools, Peel River, 66°00.36'N 134°43.19'W, *B. Bennett 00-464*, 11 July 2000 (DAO).

Between latitudes 64°N and 67°N the only site known in the Territory to Cody (1996) was adjacent to the Upper Bonnet Plume River. The Wind River site is about 130 kilometers to the northwest.

Kobresia simpliciuscula (Wahlenb.) Mack., Simple Kobresia – YUKON: Wind River, 64°48.46'N 134° 41.34'W, *B. Bennett 00-359*, 3 July 2000 (DAO); riverbar, Wind River, 65°12.49'N 135°13.17'W, *B. Bennett 00-199*, 5 July 2000 (DAO); hummocky *Picea mariana* site, Wind River, 64°58.67'N 134°47.12°W, *B. Bennett 00-299*, 4 July 2000 (B. Bennett Herbarium, photo DAO); dry tundra growing on bare solifluction ground, Vuntut National Park, 68°25.45'N 138°41. 45'W, *B. Bennett 00-1051*, 5 Aug. 2000 (DAO); open bare soil on solifluction plain, Dog Creek Ponds, Vuntut National Park, 68°26.37'N 138°45.12'W, *B. Bennett 00-1053*, 8 Aug. 2000 (DAO).

The first three specimens cited above are extensions of the known range in the Territory (Cody 1996) between latitudes 64°N and 66°N of about 175 kilometers east of the Dempster Hwy. The last two specimens cited above are intermediate between a site west of the Firth River and sites near the Northwest Territory border.

Scirpus caespitosus L. ssp. *austriacus* (Pallas) Asch. & Graebn., Tufted Clubrush – YUKON: wet area adjacent to stream in open dolomite delta, Wind River, 64°48.46'N 134°41.34'W, *B. Bennett 00-256*, 3 July 2000 (DAO).

The specimen cited above is intermediate between a site adjacent to the Upper Bonnet Plume River and sites mapped by Cody (1996) adjacent to the Dempster Hwy.

JUNCACEAE

Juncus balticus Willd. var. *littoralis* Engelm., Baltic Rush – YUKON: in meadow along brook draining warm spring, McPherson Lake, 61°52'19"N 129°36'34"W, *R. Rosie 2092*, 6 Sept. 2000 (DAO).

The specimen cited above is an extension of the known distribution in the Territory (Cody 1996) of about 150 kilometers east of a site near Ross River.

Juncus triglumis L. ssp. *albescens* (Lange) Hultén, Whitish Rush – YUKON: open solufluxion plains growing on bare soil, Dog Creek Ponds, Vuntut National Park, 68°26.37'N 138°26.37'W, *B. Bennett 00-934*, 7 Aug. 2000 (DAO).

Cody (1996) knew this taxon north of latitude 66°N in the Territory from only three sites in the far northwest. The specimen cited above was found about 75 kilometers east and southeast from those locations.

LILIACEAE

Lloydia serotina (L.) Rchb., Alp Lily – YUKON: alpine slope just above treeline, Upper Bonnet Plume River Drainage Site #103, 64°26'15"N 132°15'47"W, *J. Staniforth 00-018*, 5 July 2000 (DAO).

The specimen cited above is from a site in the Territory (Cody 1996) about 85 kilometers southeast of one between the Wind and Bonnet Plume rivers.

Maianthemum dilatatum (A. Wood) Nels. & Macbr., False Lily-of-the-valley

In Volume 6 of the *Illustrated Flora of British Columbia* (Douglas et al. 2001) this species was reported as occurring in the Yukon Territory. This was presumably based on the distribution map in the monograph of the genus *Maianthemum* (La Frankie 1986) where a triangle appeared in the extreme southwest of the Territory; however, the text says "along the Canadian coast as far north as northern British Columbia (Haines Road, Mile 45, *Taylor 1552* (GH)). Based on lack of material evidence for its presence in the Yukon and probable error in plotting which led to the only Yukon report, this species should not yet be included in the Yukon Flora.

Streptopus amplexifolius (L.) DC. ssp. *americanus* (Schultes) A. & D. Löve, Clasping Twistedstalk – YUKON: along alpine brook, Crescent Lake, 60°11'00"N 131°15'30"W, *R. Rosie 2118*, 22 July 2000 (DAO).

Cody (1996) considered this taxon to be rare in the Territory north to about latitude 63°N. The specimen cited above was found about 100 kilometers southeast of Johnson's Crossing.

Veratrum viride Ait. ssp. *eschscholtzii* (Gray) A. & D. Löve, White Hellebore – YUKON: strongly mounded lower slope, Upper Bonnet Plume River Drainage Site #155, 64°28'13"N 132°18'33"W, *J. Staniforth 00-150*, 12 July 2000 (DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). It was collected about 130 kilometers northeast of a site northeast of Mayo.

IRIDACEAE

Iris setosa Pallas ssp. *interior* (Anders.) Hultén, Wild Iris – YUKON: sand flats, highway crossing, Takhini River, W of Whitehorse, [60°51'N 135°45'W], *V.C. Brink V51225*, 6 July 1943 (UBC).

Douglas et al. (1981) considered this taxon rare in the Territory. Cody (1996) mapped two collections from near the Alaska border and one from the vicinity of Whitehorse. The specimen cited above was the basis of the Whitehorse dot that should have been about 35 kilometers to the northwest of Whitehorse adjacent to the Takhini River.

SALICACEAE

Salix alaxensis (Anderss.) Cov. ssp. *longistylis* (Rydb.) Hultén, Feltleaf Willow – YUKON: river alder, Richardson Mts., 66°50'22"N 134°56'56"W, *G. Brunner 26-00*, 17 July 2000, (YUKH, photo DAO) (determined by G. Argus).

The specimen cited above is the first of this subspecies collected between latitudes 64°N and 67°N. The nearest site known to Cody (1996) is about 80 kilometers to the northwest.

Salix arbusculoides Anderss., Little-tree Willow – YUKON: river alder, Richardson Mts., 66°50'22"N 134°56'56"W, *G. Brunner 25-00*, 17 July 2000 (DAO) (determined by G. Argus).

Cody et al. (2002) reported this species from adjacent to the Peel River about 120 kilometers to the south of the specimen cited above. Cody (1996) mapped a site about 120 kilometers to the northwest.

Salix arctica Pall., Arctic Willow – YUKON: strongly mounded lower slope, moist hummocky tundra, Upper Bonnet Plume River Drainage Site #153, 64°28'21"N 132°19'16"W, *J. Staniforth 00-155A*, 12 July 2000 (DAO) (determined G. Argus).

The specimen cited above is the easternmost yet found between latitudes 64°N and 66°N. It is from a site about 90 kilometers southeast a site mapped by Cody (1996).

Salix arctophila Cockerell, Northern Willow – YUKON: severely mounded valley floor wetland in undulating valley floor sedge meadow, Upper Bonnet Plume River Drainage Site, 64°22'47"N 132°07'52"W, *J. Staniforth 00-126 and 00-135*, 4-12 July 2000 (DAO) (determined by G. Argus).

Cody (1996) knew this species in the Territory from adjacent to the Arctic Coast, the northern Richardson Mts. and from a site at the north end of the Canol Road. Cody et al. (2001) reported it from the Patrol Range in the Ogilvie Mts. The specimens cited above were from a site about 175 kilometers northwest of the Canol Road site.

Salix commutata Bebb, Variable Willow – YUKON: in disturbed site in alpine, Crescent Lake, 60°11'00"N 131°15'30"W, *R. Rosie 2125*, 21 July 2000 (DAO) (determined by G. Argus).

Cody (1996) knew this species in the Territory only as far north as the north end of the North Canol Road and as far east as about longitude 129°W. The nearest site to the one reported above is about 175 kilometers to the northwest adjacent to the South Canol Road.

Salix fuscescens Anderss., Alaska Bog Willow – YUKON: tussock tundra, Wind River Camp #2, 64°51.83'N 134°38.85'W, *B. Bennett 00-825*, 4 July 2000 (DAO) (determined by G. Argus).

The specimen cited above is only the second known in the Territory south of latitude 66°N (Cody 1996). It is from about 175 kilometers east of a site adjacent to the Dempster Hwy.

Salix hastata L., Halbred Willow – YUKON: established riparian forest, Illytd Creek confluence with Wind River, 65°30'07"N 135°22'88"W, *B. Bennett 00-437*, 6 July 2000 (DAO); *Betula/Salix/Alnus* upland esker in gravelly soil, Wind River Camp #6, 65°40.46'N 135°11.76'W, *B. Bennett 00-858A, 00-144*, 7 July 2000 (DAO) (determined by G. Argus).

The specimens cited above are the first known to Cody (1996) between latitudes 64°N and 66°N east of the Dempster Hwy. It is about 75 kilometers south of a site north of latitude 66°N.

Salix niphoclada Rydb., (*S. brachycarpa* Nutt. ssp. *niphoclada* (Rydb.) Argus), Barren-ground Willow – YUKON: tussock tundra, Wind River Camp #2, 64°51.83'N 134°38.85'W, *B. Bennett 00-830*, 4 July 2000 (DAO); riverbar, east bank near confluence of Royal Creek, Wind River Camp #3, 65°06.83'N 134°47. 12'W, *B. Bennett 00-194*, 4 July 2000 (DAO); talus slope near river, Deception Mountain, Wind River, 65°36.03'N 135°28.44'W, *B. Bennett 00-414*, 7 July 2000 (DAO); loose talus at base of steep active scree slope, junction of Wind and Peel rivers, 65°50.48'N 135°18.25'W, *B. Bennett 00-808*, 8 July 2000 (DAO) (determined by G. Argus).

The specimens cited above are the first records in the Territory (Cody 1996) from the area east of the Dempster Hwy.

Salix polaris Wahlenb., Snow-bed Willow – YUKON: undulating upper slope, Upper Bonnet Plume River Drainage Site #125, 64°32'45"N 132°50'48"W, *J. Staniforth 00-100*, 8 July 2000 (DAO); strongly mounded lower slope, Upper Bonnet Plume River Drainage Site #153, 64°28'21"N 132°19'16"W, *J. Staniforth 00-155B*, 12 July 2000 (DAO); moist hummocky tundra, Upper Bonnet Plume River Drainage Site #118, 64°24'12.6"N 132°07'4"W, *J. Staniforth 00-083*, 7 July 2000 (DAO) (determined by G. Argus).

The specimens cited above are the easternmost yet known to Cody (1996) between latitudes 64°N and 66°N, about 110 kilometers east of the nearest known site.

Salix pseudomonticola Ball, (*S. monticola* sensu Cody 1996), Mountain Willow – YUKON: concave lower slope, spruce adjacent to river, Upper Bonnet Plume River Drainage, 64°22'26"N 132°46'40'W, *J. Staniforth 00-139*, 10 July 2000 (DAO).

Cody et al. (2002) extended the known range of this species in the Territory (Cody 1996) about 275 kilometers north of a site in the vicinity of Mayo. The specimen cited above is an extension of the known range of about 175 kilometers northeast of Mayo.

Salix richardsonii Hook., (*S. lanata* L. ssp. *richardsonii* (Hook.) Skvortsov), Richardson's Willow – YUKON: valley floor, riparian zone of small alpine creek, Upper Bonnet Plume River Drainage, 64°30'13"N 133°01' 38"W, *J. Staniforth 00-148*, 11 July 2000 (DAO); in hummocky *Picea/Salix* forest near river, McClusky Lake, Wind River, 64°34.19'N 134°25.77'W, *B. Bennett 00-376*, 2 July 2000 (DAO); bank of river, Wind River Camp #2, 64°45.05'N 134°38.75'W, *B. Bennett 00-835*, 3 July 2000 (DAO) (determined by G. Argus).

The specimens cited above are an extension of the known range in the Territory (Cody 1996) of about 100 kilometers northwest of a site adjacent to the Upper Bonnet Plume River.

Salix rotundifolia Trautv. ssp. *rotundifolia*, Round-leaf Willow – YUKON: growing amongst large black lichen covered talus on alpine barrens, "Selaginella Summit Site", 68°30'23"N 138°45'18"W, *B. Bennett 00-1122*, 4 Aug. 2000 (DAO) (determined by G. Argus).

Cody (1996) knew this rare species in the Territory, from three sites in the British Mountains and one in the southwest. The specimen cited above is an extension of the known range of about 75 kilometers southeast of a site east of the Firth River.

BETULACEAE

Alnus crispa (Drylander ex Ait.) Pursh ssp. *crispa*, Green Alder – YUKON: steep talus slope, Little Wind River/Wind River confluence, 65°22.89'N 135°26.1'W, *B. Bennett 00-837*, 5 July 2000 (DAO).

The specimen cited above is the first reported from the Wind River, it is however known from the Bonnet Plume River to the southeast and adjacent to the Peel River to the northeast and northwest (Cody 1996).

Alnus incana (L.) Moench ssp. *tenuifolia* (Nutt.) Breitung, Grey Alder – YUKON: lush *Picea glauca/ Alnus incana* established riparian thicket, Wind River Camp #4, 65°22.89'N 135°26.1'W, *B. Bennett 00-167*, 5 July 2000 (DAO).

The specimen cited above is only the second record from between latitudes 64°N and 67°N east of the Dempster Hwy. (Cody 1996). The other record is from just south of the Peel River about 75 kilometers to the northeast.

Betula neoalaskana Sarg., Alaska Birch – YUKON: *Betula neoalaskana/Salix scouleriana/S. bebbiana/ Alnus crispa* upland esker in gravelly soil, Wind River Camp #6, 65°40.46'N 135°11.76'W, *B. Bennett 00-252*, 7 July 2000 (B. Bennett Herbarium, photo DAO).

The specimen cited above is the first record between latitudes 64°15'N and 66°N (Cody 1996). The nearest site is just north of latitude 66°N about 80 kilometers to the north.

Betula occidentalis Hook., Water Birch – YUKON: forest site, amongst *Picea glauca*, Vuntut National Park, 68°25'45"N 138°41'27"W, *B. Bennett 00-1127*, 5 Aug. 2000 (B. Bennett Herbarium, photo DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). The nearest known site is about 60 kilometers to the southwest.

Betula papyrifera Marsh., Paper Birch – YUKON: Wind River, half way between Little Wind River and Illytd Creek, 65°27'N 135°24'W, *B. Bennett 00-436*, 6 July 2000 (B. Bennett Herbarium, photo DAO).

The specimen cited above of this only occassionally found species is the northernmost yet found in the Territory (Cody 1996). The nearest known site is adjacent to the southern Dempster Hwy. about 200 kilometers to the southwest.

SANTALACEAE

Comandra umbellata (L.) Nutt. ssp. *pallida* (A.DC.) Piehl, Pale Comandra – YUKON: exposed lakeshore, Kluane Lakeshore near Cultus Bay, 61°09.7'N 138°26'W, *S. Withers SW00-089*, 22 July 2000 (DAO).

This is only the fourth known site in the Territory of this species, which was considered rare by Douglas et al. (1981). The nearest known site was at the south end of Kluane Lake (Cody 1996).

POLYGONACEAE

Polygonum achoreum Blake, Striate Knotweed – YUKON: Haines Junction, 60°44'N 137°31'W, *P. Caswell PPC-2000-Y-441*, 29 Aug. 2000 (DAO).

This is not a common weed in the Territory. The nearest sites known to Cody (1996) are near the south end of Kluane Lake and in the vicinity of Whitehorse.

Polygonum aviculare L., Common Knotweed – YUKON: former experimental farm NW of Haines Junction, 60°46'N 137°35'W, *P. Caswell PPC-2000-Y-441*, 18 July 2000 (DAO).

This is not a common introduced weed in the Territory. The nearest site known to Cody (1996) is in the vicinity of Johnson's Crossing about 250 kilometers to the east.

Rumex acetosa L. ssp. *alpestris* (Scop.) A. Löve, Green Sorrel – YUKON: along edge of creek in valley wetland, Crescent Lake, 60°13'00"N 131°12'30"W, *R. Rosie 2122*, 21 July 2000 (DAO).

This taxon is rare in the Territory (Cody 1996). The nearest site to the one listed above is about 150 kilometers to the east, just west of Watson Lake.

CARYOPHYLLACEAE

Cerastium arvense L., Field Chickweed – YUKON: disturbed meadow, Wind River Camp #2, 64°45.05'N 134°38.75'W, *B. Bennett 00-833*, 3 July 2000 (DAO).

This is the northernmost specimen yet found in the Territory (Cody 1996). The nearest site to that listed above is from near the junction of the Klondike and Dempster highways about 225 kilometers to the southwest.

Minuartia dawsonensis (Britt.) House, Rock Sandwort – YUKON: vicinity of Snowdrift Camp, Vuntut National Park, 68°21.4'N 139°13.1'W, *P. Caswell PPC-2000-Y-098*, 19 June 2000 (DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). It is about 270 kilometers northwest of a site north of latitude 66°N.

Minuartia elegans (Cham. & Schlecht.) Schlecht., Northern Sandwort – YUKON: open riverbar in silt, Illytd Creek confluence with Wind River, 65°30.07'N 135°22.88'W, *B. Bennett 00-110*, 6 July 2000 (B. Bennett Herbarium, photo DAO); riverbar, Wind River Camp #4, 65°22.89'N 135°26.1'W, *B. Bennett 00-303*, 5 July 2000 (DAO); tussock tundra, Wind River Camp #2, 64°51.83'N 134°38.85'W, *B. Bennett 00-820*, 4 July 2000 (B. Bennett Herbarium, photo DAO); alpine tundra just above treeline, Upper Bonnet Plume River Drainage Site #103, 64°26'15"N 132° 15'47"W, *J. Staniforth 00-024*, 5 July 2000 (DAO).

The specimens cited above extend the known distribution in the Territory east about 225 kilometers between latitudes 64° and 66°N from a site about longitude 136°30'W (Cody 1996).

Minuartia obtusiloba (Rydb.) House, Alpine Sandwort – YUKON: moist wooded slope, Royal Creek, Wind River, 65°06.83'N 134°47.12'W, *B. Bennett 00-219*, 4 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory of about 150 kilometers east of a site adjacent to the Blackstone River (Cody 1996).

Minuartia yukonensis Hultén, Yukon Stitchwort – YUKON: talus slope near river, Deception Mountain, Wind River, 65°36.03'N 135°28.41'W, *B. Bennett 00-279*, 7 July 2000 (B. Bennett Herbarium, photo DAO).

The specimen cited above is the only record of this species between latitudes 64°N and 66°N east of the Dempster Hwy. The nearest site to this locality is about 75 kilometers to the northwest (Cody et al. 2000).

Silene acaulis L. ssp. *acaulis*, Moss Campion – YUKON: open *Picea glauca* forest, Wind River Camp #1, 64°34.43'N 134°28.88'W, *B. Bennett 00-268*, 2 July 2000 (DAO).

The specimen cited above, which is the first known from the drainage of the Wind River is an extension of the known range in the Territory (Cody 1996) of about 50 kilometers north of a site north of latitude 64°N.

Silene involucrata (Cham. & Schlecht.) Bocquet ssp. *involucrata*, Arctic Campion – YUKON: talus at edge of river, Wind River, 65°12.49'N 135°12.9'W, *B. Bennett 00-138*, 5 July 2000 (DAO).

The specimen cited above is the first known in the Territory from the area between latitude 64°N and the Peel River east of the Dempster Hwy.

Silene taimyrensis (Tolmatchev) Bocquet, Taimyr Campion – YUKON: loose talus at base of steep active shale scree slope junction of Wind and Peel rivers, 65°50.48'N 135°18.25'W, *B. Bennett 00-811*, 8 July 2000 (DAO).

The specimen cited above is the northernmost yet known in the Territory (Cody 1996). It is an extension of the known range of about 100 kilometers to the northwest from a site adjacent to the Bonnet Plume River.

Spergularia rubra (L.) J. & C. Presl, Purple Sand Spurry – YUKON: along dirt mining exploration road below treeline, Crescent Lake, 60°10'03"N 131°06' 55"W, *R. Rosie 2104*, 24 July 2000 (DAO).

The specimen of this introduced species cited above is an extension of the known range in the Territory (Cody 1996) of about 140 kilometers west of a site adjacent to Watson Lake and is an equal distance northwest to a site adjacent to the South Canol Road.

Stellaria borealis Bigelow, Boreal Starwort – YUKON: disturbed area, Wind River Camp #2, 64°45.05'N 134°38.75'W, *B. Bennett 00-189*, 3 July 2000 (DAO); in outwash delta containing round balls of clay, falcon site between Camp #10 and Taco Bar, 65°55'N 134°15'W, *B. Bennett 00-387*, 12 July 2000 (DAO).

The specimens cited above are extensions of the known range in the Territory (Cody 1996) of about 100 kilometers northeast from a site north of Mayo and 125 kilometers east of a site adjacent to the Dempster Hwy.

Stellaria longifolia Muhl., Long-leaved Chickweed – YUKON: hydric tussock tundra by rivulets, Vuntut National Park, 68°30.14'N 138°45.45'W, *B. Bennett 00-958*, 4 Aug. 2000 (DAO); rich late snowmelt meadow beside Dog Creek, Vuntut National Park, 68°29.14'N 138°50.35'W, *B. Bennett 00-955*, 4 Aug. 2000 (DAO); on lake edge with *Galium trifidum*, 68°24.24'N 138°37.58'W, *B. Bennett 00-986*, 5 Aug. 2000 (DAO); in basin bog in old oxbow on Eagle River, Eagle Plains, *R. Rosie 2133*, 18 July 2000 (DAO); *Larix laricina/Picea mariana/Carex media/ Eriophorum vaginatum* marsh, Peel River Camp #10 between Snake and Bonnet Plume rivers, 65°57.61'N 134°25.68'W, *B. Bennett 00-700*, 12 July 2000 (DAO).

The first three specimens cited above are the northernmost yet found in the Territory (Cody 1996). The last two specimens cited above are the first known between latitudes 64°N and 67°N east of the Dempster Hwy.

Stellaria media (L.) Vill., Chickweed – YUKON: flower bed at gas station, Haines Junction, 60°44'N 137°31'W, *P. Caswell PPC-2000-Y-483*, 26 Aug. 2000 (DAO).

The specimen of this introduced species cited above is intermediate between a site northwest of Kluane Lake and the vicinity of Whitehorse (Cody 1996; Cody et al. 2001).

CERATOPHYLLACEAE

Ceratophyllum demersum L., Hornwort – YUKON: floating in shallows along shore of Red River Lake, 61°00.43'N 132°21.30'W, *R. Rosie 2183*, 16 June 2000 (DAO).

Cody (1996) knew this circumpolar species in the Territory only from the Old Crow Flats and a site southeast of Mayo. Cody et al. (2000) reported a third area from Lee's Lake in the extreme southeast. The specimen cited above is from a site intermediate between the site southeast of Mayo and Lee's Lake.

RANUNCULACEAE

Aconitum delphinifolium DC. ssp. *paradoxum* (Rchb.) Hultén, Mountain Monkshood – YUKON: moist draw near spring near summit, White Mountain Summit, 60°18.36'N 133°57.24'W, *B. Bennett 00-590*, 30 July 2000 (B. Bennett Herbarium, photo DAO).

This taxon is infrequent in the south of the Territory (Cody 1996). The nearest site to the one listed above is about 115 kilometers to the north.

Anemone multifida Poir., Cut-leaf Anemone – YUKON: steep calcareous slope forming moist caves with talus, Wind River, Royal Creek, 65°06.83'N 135°06.43'W, *B. Bennett 00-265*, 3 July 2000 (DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). The nearest site is about 140 kilometers to the south, just south of latitude 64°N.

Aquilegia formosa Fisch. ex DC., Western Columbine – YUKON: along dirt mining exploration road below treeline, Crescent Lake, 60°10'40"N 131°10'00"W, *R. Rosie 2121*, 21 July 2000 (DAO).

This species was considered rare in the Territory by Douglas et al. (1981). The specimen cited above is the east-

ernmost yet found in the Territory (Cody 1996). The nearest site is about 180 kilometers to the northwest adjacent to the South Canol Road.

Delphinium glaucum S. Wats., Tall Larkspur – YUKON: open *Picea glauca* forest on old river terrace, Wind River Camp #6, 65°40.46'N 135°11.76'W, *B. Bennett 00-861*, 7 July 2000 (DAO); riparian *Picea glauca/Populus balsamifera/Alnus incana* forest, Wind River, Deception Mountain, 65°36.03'N 135°28.41'W, *B. Bennett 00-444*, 7 July 2000 (DAO).

The only site between latitudes 64°N and 66°N east of the Dempster Hwy. known to Cody (1996) was in the headwaters of the Bonnet Plume River. The nearest sites to those listed above are about 80 kilometers to the northwest.

Ranunculus aquatilis L. var. *eradicatus* Laest., White Water Buttercup – YUKON: in shallow water, WNW side of Trout Lake, Ivvavik National Park, 68°49'27"N 138°45'8"W, *J. M. Line 2000-15*, 28 July 2000 (DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). It is a range extension of about 60 kilometers from just north of longitude 68°N.

Ranunculus eschscholtzii Schlecht., Subalpine Buttercup – YUKON: strongly mounded graminoid/moss/lichen pediment with frost boils, Upper Bonnet Plume River Drainage Site #131, 64°31'19"N 132°51'39"W, *J. Staniforth 00-089*, 4-12 July 2000 (DAO); alpine meadow beside lake, Beavercrow Ridge, 60°18.38'N 124°34.834'W, *B. Bennett 98-655*, 17 Aug. 1998 (DAO).

The first specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 100 kilometers from a site just north of latitude 64°N; the second specimen is an extension of the known range of about 200 kilometers southeast of a site just west of longitude 127°W.

Ranunculus flammula L., Creeping Spearwort – YUKON: in wetland at west end of Trout Lake, 68° 49'27"N 138°45'08"W, *J. M. Line 2000-05*, 25 July 2000 (DAO); along shoreline, Trout Lake, 68°50'N 138°45'W, *J. M. Line 2000-1W*, 23 July 2000 (DAO).

The specimens cited above are the northernmost yet found in the Territory (Cody 1996). They are an extension of the known range of about 480 kilometers from a site adjacent to the southern Dempster Hwy.

Ranunculus pedatifidus Sm. ssp. *affinis* (R.Br.) Hultén, Birdfoot Buttercup – YUKON: wet area near caribou fence, vicinity of Snowdrift Camp, Vuntut National Park, 68°21.4'N 139°13.1'W, *P. Caswell PPC-2000-Y-137*, (Kluane National Park Herbarium, photo DAO).

Cody (1996) knew this species in the Territory west of longitude 136°45'W north to latitude 64°N and then disjunct to only two sites east of longitude 139°W and north of 68°N.

Thalictrum alpinum L., Alpine Meadow Rue – YUKON: in moist meadows in valley near Rudy Lakes, 60°13'00"N 131°12'30"W, *R. Rosie 2123*, 23 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 175 kilometers to the southeast from a site adjacent to the South Canol Road.

Thalictrum sparsiflorum Turcz. ssp. *richardsonii* (Gray) Cody, Few-flowered Meadowrue – YUKON: riparian area amongst shrub, Peel River, 65°57.27'N 134°38.5'W, *B. Bennett 00-399*, 11 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 60 kilometers from a site adjacent to the Bonnet Plume River. To the north the nearest sites known are adjacent to the Porcupine River.

BRASSICACEAE (CRUCIFERAE)

Arabis boivinii G. A. Mulligan, Boivin's Rockcress – YUKON: old Experimental Farm (Warden HQ), NW of Haines Junction, 60°46'N 137°35'W, *P. Caswell PPC-2000-Y-213*, 10 July 2000 (Kluane National Park Herbarium, photo DAO).

Cody et al. (2001) reported this species new to the Territory on the basis of collections from Kathleen Lake and the Dezadeash Camp Site to the southeast. The specimen cited above from about 40 kilometers to the northwest is only the third collection of this rare species in the Yukon.

Arabis codyi G. A. Mulligan, Cody's Rockcress – YUKON: route to Martha Black Peak, Kluane National Park, 60°41'N 137°33'W, *P. Caswell PPC-2000-Y-184*, 2 Aug. 2000 (DAO) (determined by G. A. Mulligan).

The specimen cited above is only the second known record in the Territory. The type specimen was collected at the Kaskawulsh Nunatak west of Kluane Lake about 20 kilometers to the southwest by D. F. and B. M. Murray in 1965. To the west it is known in the Wrangell-St. Elias National Park and Preserve in Alaska at 61°01.00'N 141°53.18'W, *M. B. Cook 9444* (DAO).

Arabis holboellii Hornem. var. *retrofracta* (Grah.) Rydb., Holboell's Rockcress – YUKON: Alsek Trail beyond Serpentine Creek, 60°43'N 139°46'W, *P. Caswell PPC-2000-Y-211*, 9 July 2000 (DAO) (determined by G. A. Mulligan).

This species was known to Cody (1996) to be frequent in the Territory north to latitude 64°N. The specimen cited above is an extension of about 60 kilometers west into Kluane National Park from sites adjacent to the Alaska Hwy.

Arabis kamtschatica (Fisch. ex DC.) Ledeb., Lyre-leaved Rockcress – YUKON: valley floor, moist shrub/graminoid/moss, Upper Bonnet Plume River Drainage Site #114, 64°24'51"N 132°23'W, *J. Staniforth 00-64*, 6 July 2000 (DAO); on gravelbar of Caribou River, 66°15.41'N 135°31.28'W, *R. Rosie 2134*, 15 July 2000 (DAO) (determined by G. A. Mulligan).

The first specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 140 kilometers northeast of a site northeast of Mayo. The second specimen is from a site intermediate between sites just north of latitude 65°N adjacent to the Dempster Hwy. and north of latitude 65°15'N.

Cardamine umbellata Greene (*C. oligosperma* Nutt. ssp. *kamtschatica* (Regel) Cody), Little Western Bittercress – YUKON: slough off Dog Creek, Vuntut National Park, 68°27.53'N 138°44.47'W, *B. Bennett 00-991*, 6 Aug. 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 450 kilometers to the north of a site adjacent to the Dempster Hwy.

Descurainia sophioides (Fisch.) O.E. Schulz, Northern Tanseymustard – YUKON: loose talus at base of steep active shale scree slope, junction of Wind and Peel rivers, Camp #7, 65°50.48'N 135°18.25'W, *B. Bennett 00-800*, 8 July 2000 (B. Bennett Herbarium, photo DAO); open recently flooded riverbar, Peel River, 65°55.97'N 135°03'W, *B. Bennett 00-100*, 9 July 2000 (B. Bennett Herbarium, photo DAO).

The specimens cited above are from sites intermediate between a site adjacent to the Dempster Hwy. (Cody 1996) and a site adjacent to the Snake River (Cody et al. 2001).

Draba albertina Greene, Slender Draba or Whitlow-grass – YUKON: undulating upper slope, small sedge meadow alongside seepage stream, Upper Bonnet Plume River Drainage Site #138, 64°32'31"N 131° 29'8"W, *J. Staniforth 00-114*, 9 July 2000 (DAO); St. Elias Trail, Kluane National Park, 60°18'N 137°03'W, *P. Caswell PPC-2000-Y-335*, 1 July 2000 (DAO) (determined by G. A. Mulligan).

The first specimen cited above is an extension of this rare species in the Territory (Cody 1996) of about 200 kilometers to the north from a site adjacent to the North Canol Road. The second specimen is the southernmost yet found in the Territory and is from a site about 50 kilometers southeast of sites near Haines Junction.

Draba borealis DC., Northern Draba – YUKON: moist hummocky tundra, undulating lower slope, Upper Bonnet Plume River Drainage Site #109, 64°28'10"N 132°04'45"W, *J. Staniforth 00-004*, 5 July 2000 (DAO); trailside beside ATV track, Wind River Camp #2, 64°45.05'N 134°38.75'W, *B. Bennett 00-246*, 3 July 2000 (DAO) (determined by G. A. Mulligan).

The specimens cited above are an extension of the known distribution in the Territory (Cody 1996) of about 175 kilometers to the northeast and about 100 kilometers north from a site northeast of Mayo.

Draba cana Rydb., Lance-leaved Whitlow-grass – YUKON: in calcareous talus near summit, east bank near confluence of Royal Creek, Wind River Camp #3, 65°06.83'N 135°06.43'W, *B. Bennett 00-159*, 3 July 2000 (DAO) (determined by G. A. Mulligan).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 150 kilometers east of sites adjacent to the Dempster Hwy. and north of sites just south of latitude 64°N.

Draba cinerea Adams – YUKON: subalpine meadow with *Vaccinium caespitosum* on mesic slope with *Pinus contorta*, *Abies lasiocarpa* and *Alnus incana*, Kotaneelee Range, 60°14'31"N 124°07'19"W, *B. Bennett 98-598*, 19 June 1998 (B. Bennett Herbarium, photo DAO); windblown ridge, submesic, rocky, Kotaneelee Range, 60°13'08"N 124°06'36"W, *B. Bennett 98-047*, 20 June 1998 (B. Bennett Herbarium, photo DAO) (determined by G. A. Mulligan).

The specimens cited above are an extension of the known range in the Territory of about 190 kilometers east of a site west of longitude 127°W (Cody 1996).

Draba incerta Payson, Yellowstone Whitlow-grass – YUKON: in dry *Dryas*/lichen on mountain top, Richardson Mts., 66°38'N 135°47'W, *R. Rosie 2137*, 11 July 2000 (DAO); upper talus slope in alpine, Deception Mtn., Wind River, 65°36.03'N 135°28.41'W, *B. Bennett 00-415A*, 7 July 2000 (DAO) (determined by G. A. Mulligan).

The specimens cited above are from about 75 kilometers northwest and southwest of a site known to Cody (1996) just north of latitude 66°N.

Draba kananaskis G. A. Mulligan, Longstalk Whitlow-grass (Figure 3) – YUKON: moist draw east of Dog Creek Camp, 68°27.53'N 138°44.47'W, *B. Bennett 00-994*, 4 Aug. 2000 (DAO) (determined by G. A. Mulligan).

The specimen cited above is a new record for the Yukon Territory. This is an extension of the known range of about 900 kilometers north of sites in Wrangell-St. Elias National Park and Preserve in southeastern Alaska. A previous record (*Cody & Ginns 33149*, 4 July 1984, from the Ogilvie Mts.) orginally identified as *D. kananakis* by Mulligan was revised by him to *D. longipes* in 1986.

FIGURE 3. *Draba kananaskis* G. A. Mulligan, Longstalk Whitlow-grass (drawn by Lee Mennell).

Draba macounii O.E. Schulz, Macoun's Draba or Whitlow-grass – YUKON: undulating upper talus slope, Upper Bonnet Plume River Drainage Site #117, 64°24'27"N 132°08'7"W, *J. Staniforth 00-069*, 7 July 2000 (DAO).

The specimen cited above is an extension of the known distribution in the Territory (Cody 1996) of about 130 kilometers to the northeast of a site northeast of Mayo.

Draba porsildii G. A. Mulligan – YUKON: Pikatak Nunatak near Queen Mary Glacier, Kluane National Park, elevation over 8000 feet, *P. Caswell PPC-2000-Y-345*, 13 July 2000 (DAO) (determined by G. A. Mulligan).

This is a rare species in the Territory (Douglas et al. 1981). The specimen cited above from a site west of three previously known sites in the park represents the sixth location in the Territory (Cody 1996).

Draba scotteri G. A. Mulligan – YUKON: Rock Glacier, Kluane National Park, 60°25'N 137°05'W, *P. Caswell PPC-2000-Y-314*, 13 Aug. 2000 (DAO); Alsek Trail, Kluane National Park, 60°45'N 137°46'W, *P. Caswell PPC-2000-Y-348*, 8 June 2000 (DAO) (determined by G. A. Mulligan).

Douglas et al. (1981) considered this species rare in the Territory. The first specimen cited above extends the known range in the Territory about 50 kilometers southeast in the Park.

Erysimum cheiranthoides L., Wormseed Mustard – YUKON: slumping eroding banks, cobbles and silty muck, Wind River, 65°47.45'N 135°13'W, *B. Bennett 00-122*, 8 July 2000 (DAO); riverbar, Peel River Camp #10, between Snake and Bonnet Plume rivers, 65°57. 61'N 134°25.68'W, *B. Bennett 00-704*, 12 July 2000 (DAO) (determined by G. A. Mulligan).

The specimens cited above are an extension of the known range in the Territory (Cody 1996) of about 150 kilometers east of a site adjacent to the Dempster Hwy.

Lepidium sativum L., Garden Cress – YUKON: old experimental farm NW of Haines Junction, 60°46'N 137°35'W, *P. Caswell PPC-2000-Y-405*, 2 July 2000 (DAO) (determined by G. A. Mulligan).

This introduced species was previously known in the Territory (Cody 1996) only from the vicinity of Dawson.

Lesquerella arctica (Wormsk. ex Hornem.) S. Watson ssp. *arctica*, Arctic Bladderpod – YUKON: undulating lower slope, *Dryas* outwash floodplain, Upper Bonnet Plume River Drainage Site #110, *J. Staniforth 00-049*, 6 July 2000 (DAO); open dolomite delta, Wind River, 64°48.46'N 134°41.34'W, *B. Bennett 00-223*, 3 July 2000 (B. Bennett Herbarium, photo DAO); calcareous scree, Wind River Camp #2, 64°51.83'N 134°85'W, *B. Bennett 00-823*, 4 July 2000 (DAO) (determined by G. A. Mulligan).

The specimens cited above are intermediate between sites adjacent to northern South Canol Road and a site just south of latitude 68°N (Cody 1996).

Lesquerella calderi Mulligan & Porsild (*L. arctica* (Wormsk. ex Hornem.) S. Watson ssp. *calderi* (Mulligan & Porsild) Hultén) – YUKON: vicinity of Snowdrift Camp, Vuntut National Park, 68°21.4'N 139°13.1'W, *P. Caswell PPC-2000-Y-093*, 19 June 2000 (DAO) (determined by G. A. Mulligan).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). It is from a site about 110 kilometers NNW of a site near the Mackenzie border just north of latitude 68°N.

Subularia aquatica L. ssp. *americana* Mulligan & Calder, Awlwort – YUKON: on sandy/gravelly shore of Davis Lake in valley of Eagle River, 66°11.06'N 136°25.00'W, *R. Rosie 2138*, 18 July 2000 (DAO) (determined by G. A. Mulligan).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 480 kilometers northwest from a site adjacent to the North Canol Road.

SAXIFRAGACEAE

Leptarrhena pyrolifolia (D. Don) Ser., Leather-leaved Saxifrage – YUKON: along alpine brook, Crescent Lake, 60°11'00"N 131°15'30"W, *R. Rosie 2127*, 21 July 2000 (DAO).

The specimen cited above is the southernmost yet found in the Territory (Cody 1996). The nearest sites are near the northern South Canol Road about 175 kilometers to the northwest and in the vicinity of Frances Lake about 190 kilometers to the northeast. To the south it is frequent throughout much of British Columbia.

Parnassia fimbriata Koenig, Fringed Grass-of-Parnassus – YUKON: moist rivulet on east-facing mountain, Wind River Camp #1, 64°40.39'N 134°35. 96'W, *B. Bennett 00-759*, 2 July 2000 (B. Bennett Herbarium, photo DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). The nearest known site is about 125 kilometers to the southwest in the vicinity of Mayo.

ROSACEAE

Dryas crenulata Juz. – YUKON: moist hummocky tundra, Upper Bonnet Plume River Drainage Site #118, 64°24'12.6"N 132°07'4"W, *J. Staniforth 00-084*, 7 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory of about 100 kilometers to the southeast from a site adjacent to the Bonnet Plume River.

Dryas hookeriana Juz., Hooker's Mountain Avens – YUKON: Richardson Mts., 66°52'12"N 135°50'29"W, *G. Brunner 17A-00*, 16 July 2000 (YUKH, photo DAO).

The specimen cited above is intermediate between a site west of the Wind River at latitude 65°16'N and a site near the Firth River at latitude 69°12'N (Cody et al. 2000).

Fragaria virginiana Duchesne ssp. *glauca* (S. Wats.) Staudt, Wild Strawberry – YUKON: riverbar, spreading in loose sand, Peel River Camp #8, 65°56.03'N 134°56.03'W, *B. Bennett 00-769*, 9 July 2000 (DAO); loose sand near top of beach, Peel River, Taco Bar, 66°00.15'N 134°13'W, *B. Bennett 00-397*, 13 July 2000 (DAO).

The specimens cited above are the northernmost yet found in the Territory and are north of a site adjacent to the northern Bonnet Plume River (Cody 1996; Cody et al. 2000).

Potentilla nivea L., Snow Cinquefoil – YUKON: in dry *Dryas*/ lichen on mountain top, Richardson Mts., 66° 51'N 135°51'W, *R. Rosie 2156*, 16 July 2000 (DAO).

The nearest site to the specimen cited above is about 100 kilometers from a site to the north and to the south about 300 kilometers to the southern Dempster Hwy.

Rosa woodsii Lindl., Western Rose – YUKON: dry steep slope below cliffs near coal mine shaft, Tantalus Butte, Carmacks, 67°07.23'N 136°15.23'W, *B. Bennett 00-1101*, 30 May 2000 (B. Bennett Herbarium, photo DAO).

Douglas et al. (1981) considered this species rare in the Territory. The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 160 kilometers to the northwest from the vicinity of Whitehorse.

Rubus pedatus J. E. Sm., Creeping Raspberry – YUKON: along dirt road near Crescent Lake, 60°11'41"N 131°13'01"W, *R. Rosie 2124*, 21 July 2000 (DAO).

This rare species in the Territory was known to Douglas et al. (1981) and Cody (1996) from a single collection in the vicinity of Bennett Lake. The specimen cited above is an extension of the known range of about 200 kilometers to the east.

Rubus pubescens Raf., Dwarf Raspberry – YUKON: in meadow along brook draining warm spring, McPherson Lake, 61°52'19"N 129°36'34"W, *R. Rosie 2095*, 6 Sept. 2000 (DAO).

Cody et al. (1998) extended the known distribution in the Territory (Douglas et al. 1981) north to the vicinity of Frances Lake. The specimen cited above is a further extension of about 40 kilometers to the north.

Sanguisorba canadensis L. ssp. *latifolia* (Hook.) Calder & Taylor, Canadian Burnet – YUKON: along gravelly/sandy beach near warm spring, McPherson Lake, 61°52'19"N 129°36'34"W, *R. Rosie 2096*, 6 Sept. 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 80 kilometers northwest of a site adjacent to the Nahanni Range Road.

Sibbaldia procumbens L., Sibbaldia – YUKON: strongly mounded-graminoid/moss/lichen pediment with frost boils, Upper Bonnet Plume River Drainage Site #131, 64°31'19"N 132°51'39"W, *J. Staniforth 00-090*, 4-12 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 175 kilometers from a site adjacent to the North Canol Road and northeast of sites north of Mayo.

FABACEAE (LEGUMINOSAE)

Astragalus bodinii Sheldon, Bodin's Milk-vetch – YUKON: huge riverbar system, Peel River Camp #8, 65°56.3'N 134°58.84'W, *B. Bennett 00-768*, 9 July 2000 (DAO).

The specimen cited above is the only specimen in the Territory (Cody 1996) from between latitudes 64°N and 67°N east of the Dempster Hwy.

Astragalus cicer L., Chick-pea Milk-vetch – YUKON: disturbed area near tailings dam, Sa Dena Hes Mine Site, 60°32.8'N 128°51.8'W, *S. Withers SW00-179*, 31 Aug. 2000 (DAO).

Cody et al. (1998) reported the first record of this introduced species in the La Biche area of the Territory and Cody et al. (2001) confirmed a large population along the Haines Road in the vicinity of Klukshu. The specimen cited above is an extension of the range about 280 kilometers to the west of the La Biche site.

Astragalus tenellus Pursh, Pulse Milk-vetch – YUKON: tussock tundra, Wind River, 64°44.63'N 134°38.3'W, *B. Bennett 00-183*, 3 July 2000 (B. Bennett Herbarium, photo DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). It is an extension of the known range of about 115 kilometers to the northeast from a site south of latitude 64°N.

Hedysarum boreale Nutt. ssp. *mackenzii* (Richards.) Welsh f. *niveum* (Boivin) Cody, Boreal Sweet-vetch – YUKON: vicinity of Snowdrift Camp, Vuntut National Park, 68°21.4'N 139°13.1'W: *P. Caswell PPC-2000-Y-082*, 22 June 2000 (DAO).

This white-flowered form was only known from two localities in the Territory at the time the flora (Cody 1996) was written (Pine Creek [67°51'N 137°53'W type locality] and Richardson Mts., 66°08'N 135°51'W).

Lotus corniculatus L., Birds-foot Trefoil – YUKON: disturbed area near tailings dam, Sa Dena Hes Mine Site, 60°32.8'N 128°51.8'W, *S. Withers SW00-180*, 31 Aug. 2000 (DAO).

This introduced species from Eurasia is new to the Flora of the Yukon Territory. It is found across Canada from Newfoundland to British Columbia. The genus *Lotus* can be separated from the genera *Oxytropis* and *Astragalus* as follows:

A. Flowers axillary, solitary or in small stalked heads or umbels; free portion of filaments (sometimes only every other one) dilated and usually broader than the anthers ..... *Lotus*

A. Flowers in spikes or racemes; none of the filaments dilated ..... *Astragalus* and *Oxytropis*

Onobrychis viciifolia Scop., Sainfoin – YUKON: disturbed area near tailings dam, Sa Dena Hes Mine Site, 60°32.8'N 128°51.8'W, *S. Withers SW00-178*, 31 Aug. 2000 (DAO).

This introduced species was known to Cody (1996) and Cody et al. (2002) only from the vicinity of Whitehorse. The specimen cited above is from a site about 350 kilometers to the east.

Oxytropis campestris (L.) DC. ssp. *roaldii* (Ostenf.) Cody – YUKON: shrubby riverbar, Wind River Outfitter's Camp, 64°34.43'N 134°28.88'W, *B. Bennett 00-233*, 2 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 180 kilometers east of a site adjacent to the Dempster Hwy.

Oxytropis nigrescens (Pall.) Fisch. ssp. *nigrescens*, Blackish Locoweed – YUKON: alpine slope, Upper Bonnet Plume River Drainage Site #100, 64°20'20"N 132°16'26"W, *J. Staniforth 00-006*, 5 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 80 kilometers east of a site adjacent to the upper Wind River.

Trifolium pratense L., Red Clover – YUKON: dry roadside, Alaska Hwy. near Swift River, 60°00.3'N 131° 06.0'W, *S. Withers SW00-175*, 30 Aug. 2000 (DAO).

The specimen cited above is an extension of known range of this introduced species in the Territory (Cody 1996) of about 125 kilometes east of the vicinity of Johnson's Crossing.

VIOLACEAE

Viola epipsila Ledeb. ssp. *repens* (Turcz.) Becker, Dwarf Marsh Violet – YUKON: in moist meadow in valley near Rudy Lakes, 60°13'00"N 131°12'30"W, *R. Rosie 2129*, 23 July 2000 (DAO).

The specimen cited above is from a site intermediate between southern Canol Road and the vicinity of Watson Lake (Cody 1996).

Viola langsdorfii (Regel) Fisch., Alaska Violet – YUKON: undulating lower slope, patches of shrubs amidst forb meadows, Upper Bonnet Plume River Drainage Site #129, 64°31'26"N 132°49'52"W, *J. Staniforth 00-103*, 8 July 2000 (DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996) about 230 kilometers northwest of a site just south of the north end of the Canol Road. It is a rare species in the Territory.

Viola nephrophylla Greene, Northern Bog Violet – YUKON: in meadow along brook draining warm spring, McPherson Lake, 61°52'19"N 129°36'34"W, *R. Rosie 2100*, 6 Sept. 2000 (DAO).

This is a rare species in the Territory that Douglas et al. (1981) knew only from the vicinity of Watson Lake. Cody et al. (1998, 2000) reported new sites from the Beaver River and Mount Billings. The specimen cited above is an extension of the known range about 100 kilometers northwest of Mount Billings.

ONAGRACEAE

Circaea alpina L. ssp. *alpina,* Enchanter's Nightshade – YUKON: in meadow along brook draining warm spring, McPherson Lake, 61°52'19"N 129°36'34"W, *R. Rosie 2094*, 6 Sept. 2000 (DAO).

Douglas et al. (1981) knew this rare species in the Territory from a single collection from the Beaver River. Cody et al. (1998) reported new sites from the La Biche River and Frances Lake. The specimen cited above is an extension of about 60 kilometers northwest of Frances Lake.

Epilobium hornemannii Rchb., Hornemann's Willowherb – YUKON: strongly mounded undulating alpine valley lower slope, Upper Bonnet Plume River Drainage Site #154, 64°28'19"N 132°19'21"W, *J. Staniforth 00-152*, 12 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory of about 130 kilometers east of a site between latitudes 64°N and 66°N west of longitude 135°W.

Epilobium palustre L., Swamp Willowherb – YUKON: *Larix laricina/Picea mariana/Carex media/Eriophorum* marsh, Peel River Camp #10 between Snake and Bonnet Plume rivers, 65°57.61'N 134°25.68'W, *B. Bennett 00-707*, 12 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 75 kilometers east of the only known site between latitudes 64°N and 67°N.

APIACEAE (UMBELLIFERAE)

Cicuta maculata L. var. *angustifolia* Hook., Spotted Water-hemlock – YUKON: in meadow along brook draining warm spring, McPherson Lake, 61°52'19"N 129°36'34"W, *R. Rosie 2083*, 6 Sept. 2000 (DAO).

This is a rare species in the Yukon Territory (Douglas et al. 1981). The specimen cited above is an extension of the known range in the Territory (Cody 1996; Cody et al. 2000) of about 230 kilometers northwest of a site west of longitude 127°W.

Osmorhiza depauperata Phil., Blunt-fruited Sweetcicely – YUKON: Rock Glacier, Kluane National Park, 60°25'N 137°05'W, *P. Caswell PPC-2000-Y-428*, 13 Aug. 2000 (Kluane National Park, photo DAO); same lcoality *P. Caswell 437* (ALA, photo DAO); in *Salix barclayi* stand on outwash fan, ca. 3 mi. SW of Onion Lake, 60°6'N 137°30'W, *H.L. & I.J. Weaver 235*, 18 July 1975 (photo DAO).

Cody (1996) knew this species only in the southeast of the Territory. The specimens cited above are an extension of the known range of about 375 kilometers to the west. It is however known in northwestern British Columbia and adjacent Alaska.

PYROLACEAE

Pyrola minor L., Lesser Wintergreen – YUKON: on small plateau above lake, S side of Trout Lake, 68° 49'27"N 138°45'8"W, *J. M. Line 2000-26*, 25 July 2000 (DAO).

Cody (1996) knew this species in the Territory only as far north as about 64°30'N. Cody et al. (2001) extended the range northward to 66°49'N. The specimen cited above is a further northward extension of about 280 kilometers northwest of the Vittrewka Lake site.

ERICACEAE

Andromeda polifolia L., Bog Rosemary – YUKON: undulating lower slope, spruce/shrub/lowshrub/forb/moss, Upper Bonnet Plume River Drainage Site #105, 64°26'6"N 132°15'28"W, *J. Staniforth 00-001*, 5 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 100 kilometers southeast of a site adjacent to the Bonnet Plume River.

Kalmia polifolia Wang., Bog-laurel – YUKON: undulating upper slope, small sedge meadow alongside seepage stream, Upper Bonnet Plume River Drainage near site #138, 64°32'31"N 131°29'8"W, *J. Staniforth 00-115*, 9 July 2000 (DAO).

The specimen cited above is extension of the known range in the Territory (Cody 1996) of about 130 kilometers east of a site west of longitude 135°W.

PRIMULACEAE

Primula egaliksensis Wormsk., Greenland Primrose – YUKON: riverbar, Wind River Camp #1, 64°40.39'N 134°35.96'W, *B. Bennett 00-750*, 2 July 2000 (DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). The nearest site is adjacent to the northern part of the South Canol Road about 350 kilometers to the south.

MENYANTHACEAE

Menyanthes trifoliata L., Buckbean – YUKON: in basin bog in old oxbow on Eagle River, Eagle Plains, 66° 16'N 136°31'W, *R. Rosie 2154*, 18 July 2000 (DAO).

The specimen cited above is from a site intermediate between a site adjacent to the Porcupine River about 150 kilometers to the northwest and about 200 kilometers to the southwest adjacent to the Dempster Hwy. (Cody 1996).

POLEMONIACEAE

Phlox hoodii Richards., Moss Phlox – YUKON: hummock tussock tundra, Wind River, 64°54'2"N 134°41'25"W, *B. Bennett 00-164*, 4 July 2000 (DAO); vicinity of Snowdrift Camp, 68°21.4'N 139°13.1'W, *P. Caswell PPC-2000-Y-121*, 22 June 2000 (DAO).

The specimens cited above are the northernmost yet found in the Territory (Cody 1996). The first specimen is an extension of about 225 kilometers to the northeast from a site adjacent the southern Dempster Hwy. and the second specimen is a further extension of about 450 kilometers to the north.

Polemonium acutiflorum Willd., Tall Jacob's-ladder – YUKON: strongly mounded undulating alpine valley hh#154, 64°28'19"N 132°19'21"W, *J. Staniforth 00-151*, 12 July 2000 (DAO); undulating upper slope, moist hummocky tundra, Upper Bonnet Plume River Drainage Site #108, 64°28'05"N 132°4'15"W, *J. Staniforth 00-034*, 5 July 2000 (DAO).

The specimens cited above are an extension of the known range in the Territory (Cody 1996) of about 140 kilometers northeast of a site just west of longitude 135°W.

BORAGINACEAE

Eritrichium splendens Kearney, Showy Alpine Forget-me-not – YUKON: in steep loose talus, east bank confluence of Royal Creek, Wind River Camp #3, 65°06.83'N 134°47.12'W, *B. Bennett 00-220*, 4 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 150 kilometers east of a site adjacent to the Dempster Hwy.

Lappula occidentalis (Wats.) Greene, Western Stickseed – YUKON: common along disturbed roadsides, Dempster Hwy., 65°09.19'N 138°21.4'W, *B. Bennett 00-074*, 10 June 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory of about 140 kilometers north of sites in the vicinity of Dawson City.

VERBENACEAE

Verbena hastata L., Blue Vervain (Figure 4) – YUKON: roadside established and spreading, highway adjacent to former Experimental Farm, Haines Junction, 61° 46'30"N 137°33'W, *P. Caswell s.n.*, 13 Aug. 2000 (B. Bennett Herbarium, photo DAO).

The family Verbenaceae is new to the Territory (Cody 1996). It resembles the mint family in having an ovary that ripens into 2-4 seed-like nutlets. It can be separated from the family Lamiaceae (Labiatae) as follows:

A. Anthers 4, in pairs; ovary not deeply 4-lobed; stems round ..... Verbenaceae
A. Anthers 2-4, rarely 3, ovary deeply 4-lobed; stems often square ..... Lamiaceae

FIGURE 4. *Verbena hastata* L., Blue Vervain (drawn by Lee Mennell).

Verbena hastata is an erect perennial; stems to 1 m or more, branched above, pubescent; leaves lanceolate or lance-oblong to narrowly ovate, to 18 cm long, acuminate, coarsely incised-serrate, scrabrous-pubescent; spikes strict, pencil-like, usually numerous in a panicle, compact, with mostly imbricated fruiting calyxes, bracts lance-subulate, mostly shorter than the pubescent calyx (2.5-3 mm long); calyx with finally incurving subulate-tipped lobes; corolla-limb violet-blue, 3-4.5 mm broad; nutlets 2 mm long, nearly smooth or faintly striate. Nova Scotia to southern British Columbia, south to Florida, Texas and California.

LAMIACEAE (LABIATAE)

Prunella vulgaris L. ssp. *lanceolata* (Bart.) Hultén, Heal-all (Figure 5) – YUKON: along gravelly/sandy beach near warm spring/McPherson Lake, 61°52'19"N 129°36'34"W, *R. Rosie 2093*, 6 Sept. 2000 (DAO).

Prunella vulgaris ssp. *lanceolata* is the North American component of a circumpolar species which is new to the flora of the Yukon Territory (Cody 1996). The genus *Prunella* can be separated from *Galeopsis* and *Stachys* as follows:

A. Calyx deeply bilabiate, ten-nerved, reticulate-veiny, closed in fruit, the upper lip flat and 3-toothed ..... *Prunella*
A. Calyx not strongly bilabiate, open in fruit, the lobes or teeth sub-equal .... *Galeopsis* and *Stachys*

Prunella vulgaris ssp. *lanceolata* has a stem ascending or erect from a short rhizome; leaves lanceolate to oblong, gradually narrowed or cuneate at base, shallowly dentate; bracts

FIGURE 5. *Prunella vulgaris* L. ssp. *lanceolata* (Bart.) Hultén, Heal-all (drawn by Lee Mennell).

ciliate; moist open woods, fields and roadsides; Newfoundland to British Columbia and Alaska and south to Florida, Texas and California.

SCROPHULARIACEAE

Castilleja pallida (L.) Spreng. var. *caudata* (Pennell) Boivin, *C. caudata* (Pennell) Rebr., Port Clarence Paintbrush – YUKON: moist pockets in talus, Kotaneelee Range, 60°14.31'N 124°07.19'W, *B. Bennett 98-567*, 19 June 1998 (B. Bennett Herbarium, photo DAO) (determined by M. Egger).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 550 kilometers east of a site in the vicinity of Carcross.

Linaria vulgaris Miller, Butter-and-eggs, Yellow-toadflax – YUKON: Haines Junction, 60°44'N 137°31'W, *L. Freese PPC-2000-4-408*, 20 July 2000 (DAO).

The specimen cited above of this introduced species is from only the fourth known locality in the Territory (Cody 1996).

Mimulus guttatus DC., Yellow Monkeyflower – YUKON: in meadow along brook draining warm spring, McPherson Lake, 61°52'19"N 129°36'34"W, *R. Rosie 2098*, 6 Sept. 2000 (DAO).

This species was considered rare in the Territory by Douglas et al. (1981). The specimen cited above is from the northernmost site yet found in the Territory (Cody 1996; Cody et al. 1998), about 40 kilometers north of a site in the vicinity of Frances Lake.

Pedicularis lanata Cham. & Schlecht., Woolly Lousewort – YUKON: severely mounded lower slope tussock tundra, Upper Bonnet Plume River Drainage Site #140, 64°19'23"N 131°35'19"W, *J. Staniforth 00-118*, 14 July 2000 (DAO); undulating upper slope, moist hummocky tundra, Upper Bonnet Plume River Drainage Site #109, 64°28'10"N 132°04'45"W, *J. Staniforth 00-005, 00-009*, 5 July 2000 (DAO).

The specimens cited above are the easternmost yet found between latitudes 64°N and 66°N. They are about 140 kilometers southeast of a site about the middle of the Bonnet Plume River drainage.

OROBANCHACEAE

Orobanche fasciculata (Cham. & Schleht.) Fedtsch, Ground-cone – YUKON: breakwater of Slim's River Causeway, 60°59.5'N 138°29'W, *P. Caswell PPC-2000-Y-427* (Kluane National Park Herbarium, photo DAO).

This species was considered rare in the Territory by Douglas et al. (1981). The specimen cited above is an extension of the known distribution in the Territory (Cody 1996) of about 190 kilometers west of the vicinity of Whitehorse.

LENTIBULARIACEAE

Utricularia minor, Lesser Bladderwort – YUKON: in small stagnant slough in the middle of *Eriophorum* tussock tundra habitat between Trout Lake and the Babbage River, 68°49'N 138°45'W, *J. M. Line 2000-12*, 28 July 2000 (DAO).

Cody (1996) knew this rare species in the Territory only as far north as about latitude 64°30'N adjacent to the Dempster Hwy. The specimen cited above is an extension of the known distribution of about 475 kilometers to the north.

PLANTAGINACEAE

Plantago major L., Common Plantain – YUKON: parking lot, Auriol Trail, Kluane National park, 60°42'N 137°27'W, *P. Caswell PPC-2000-4-440*, 4 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 115 kilometers west of the vicinity of Whitehorse.

RUBIACEAE

Galium trifidum L., Small Bedstraw – YUKON: in basin bog in old oxbow on Eagle River, 66°16'N 136°31'W, *R. Rosie 2157*, 18 July 2000 (DAO).

The specimen cited above is intermediate between a site adjacent to the Dempster Hwy. about 160 kilometers to the southwest and a site adjacent to the Bell River about 140 kilometers to the north (Cody 1996).

ADOXACEAE

Adoxa moschatellina L., Moschatel – YUKON: alder/rose, Richardson Mts., 66°44'51"N 135°24'W, *G. Brunner 24B-00*, 17 July 2000, (YUKH, photo DAO).

Cody knew this species in the Territory (1996) as far north as the southern Dempster Hwy. and then disjunct to the Porcupine River near the Alaska border. The specimen cited above

is an extension of the known range about 260 kilometers northeast of the Dempster sites and 240 kilometers southeast of the Porcupine River site.

ASTERACEAE (COMPOSITAE)

Antennaria rosea Greene ssp. *confinis* (Greene) Bayer – YUKON: in open meadow under *Salix* near outfitter cabin, McClusky Lake, Wind River, 64°34.19'N 134°25.77'W, *B. Bennett 00-343*, 2 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 125 kilometers northeast of a site in the vicinity of Mayo.

Arnica angustifolia Vahl ssp. *attenuata* (Greene) Douglas & Ruyle-Douglas, Alpine Arnica – YUKON: undulating lower slope, open spruce/lichen/grass/forb, Upper Bonnet Plume River Drainage Site #147, 64°22'38"N 132°47'W, *J. Staniforth 00-141*, 10 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 130 kilometers northeast of a site northeast of Mayo.

Arnica chamissonis Less. ssp. *chamissonis*, Meadow Arnica – YUKON: roadside in open white spruce forest near Canyon Lake, 61°09'N 136°58.2'W, *S. Withers SW00-156*, 6 Aug. 2000 (DAO); in meadow along brook draining warm spring, McPherson Lake, 61° 52'19"N 129°36'34"W, *R. Rosie 2086*, 6 Sept. 2000 (DAO).

The specimens cited above are northern extensions of the range of this rare subspecies in the Territory (Cody 1996; Cody et al. 2000). The first specimen is an extension of about 60 kilometers northeast from the vicinity of Haines Junction and the second specimen is an extension of about 40 kilometers northwest from the vicinity of Frances Lake.

Arnica griscomii Fern. ssp. *frigida* (C. A. Mey. ex Iljin) S. J. Wolf, Snow Leopardbane – YUKON: undulating upper slope, steep alpine ridge, rock, rubble, bare soil and sparse vegetation, Upper Bonnet Plume River Drainage Site #125, 64°32'45"N 132°50'48"W, *J. Staniforth 00-101*, 8 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 100 kilometers east of a site just west of the Wind River.

Artemisia dracunculus L., Tarragon – YUKON: damp open meadow with dwarf birch, Meadow near Atthilu Lake, 61°14.2'N 136°55.9'W, *S. Withers SW00-148*, 5 Aug. 2000 (DAO); near Aishihik Lake at south end of lake, 61°25'N 137°15'W, *G. Brunner 496-01*, 12 Aug. 2001 (DAO); very common in an area covering about 100 square meters on both sides of the road, Giltana Slough, Aishihik Valley, 61°14'04"N 136° 57'22"W, *B. Bennett 01-064*, 11 Aug. 2001 (DAO).

This species which is restricted to southwestern Yukon (Cody 1996) was considered rare in the Territory by Douglas et al. (1981). The specimens cited above are an extension of the known range of about 60 kilometers northeast of the vicinity of Haines Junction.

Aster modestus Lindl. in DC., Western Bog Aster – YUKON: in meadow along brook draining warm spring, McPherson Lake, 61°52'19"N 129°36'34"W, *R. Rosie 2087*, 6 Sept. 2000 (DAO).

This species was considered rare in the Territory by Douglas et al. (1981). The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 230 kilometers northwest of a site east of Watson Lake.

Bidens cernua L., Nodding Beggarticks – YUKON: Horseshoe Slough Habitat Protection Area near Mayo, 63°26'N 135°06'W, *D. Mossop 16*, July 2000 (DAO).

Douglas et al. (1981) considered this species which was known only from a single site in the extreme southeast adjacent to the Beaver River as rare in the Territory. The specimen cited above is an extension of the known range of about 700 kilometers to the northwest.

Chrysanthemum integrifolium Richards., Entire-leaved Daisey – YUKON: undulating lower slope, shrub thicket with pockets of lichen, Upper Bonnet Plume River Drainage Site #111, 64°22'10"N 132°19'49"W, *J. Staniforth 00-051*, 6 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 180 kilometers southeast of a site between the Wind and Bonnet Plume rivers.

Hieracium albiflorum Hook., White Hawkweed (Figure 6) – YUKON: along dirt mining exploration road on mountain slope, Crescent Lake, 60°10'03"N 131°06' 55"W, *R. Rosie 2106*, 24 July 2000 (DAO).

Cody (1996) suggested that this species should be looked for in southwestern Yukon. It has now been found and should be added to the list of rare species (Douglas et al. 1981).

Matricaria perforata Mérat., Scentless Mayweed – YUKON: disturbed area near tailings dam, Sa Dena Hes Mine Site, 60°32.8'N 125°51.8'W, *S. Withers SW00-177*, 31 Aug. 2000 (DAO); open roadside, Faro Mine Road, 62°21.6'N 133°25'W, *S. Withers SW00-250*, 5 Sept. 2000 (DAO); disturbed area by road, Caribou Lake Road, 60°31.1'N 134°19.5'W, *S. Withers SW00-164*, 7 Aug. 2000 (DAO).

Cody (1996) knew this introduced species from only the vicinities of Frances Lake and Ross River. Cody et al. (2000, 2002) added additional sites to Nisutlin Delta and by the Top of the World Hwy. It is now becoming more widespread in disturbed areas.

Senecio indecorus Greene, Rayless Mountain Butterweed – YUKON: gravelly riverbar, Wind River Camp #6, 65°40.46'N 135°11.76'W, *B. Bennett 00-849*, 7 July 2000 (DAO).

The specimen cited above is the northernmost yet found in the Territory (Cody 1996). It is an extension of about 250 kilometers north of sites in the vicinity of Stewart Crossing.

Senecio sheldonensis A.E. Porsild, Mount Sheldon Ragweed – YUKON: convex mid slope, Upper Bonnet Plume River Drainage Site #128, 64°32'37"N 132°50'26"W, *J. Staniforth 00-095*, 8 July 2000 (DAO).

The specimen cited above is from a location about 60 kilometers southeast of the northernmost site mapped by Cody (1996) adjacent to the Bonnet Plume River.

Senecio streptanthifolius Greene, Rocky Mountain Groundsel – YUKON: steep active solifluxion slope across river from camp, Wind River Camp #1, 64°40.39'N 134°35.96'W, *B. Bennett 00-173*, 3 July 2000 (DAO); riverbar, Wind River Camp #6, 65°40.46'N 135°11.76'W, *B. Bennett 00-857*, 7 July 2000 (DAO).

The specimens cited above are the northernmost yet found in the Territory (Cody 1996), about 200 kilometers north of a site northeast of Mayo.

Senecio tundricola Tolm., Tundra Ragwort – YUKON: convex lower slope, open willow/lichen/moss, Upper Bonnet Plume River Drainage near Site #137, 64°31'57"N 131°32'42"W, *J. Staniforth 00-116*, 9 July 2000 (DAO).

The specimen cited above is the easternmost yet found in the Territory. It is from a site about 240 kilometers east of a site just east of the Hart River.

Senecio vulgaris L., Common Groundsel – YUKON: flower bed at Kluane Park Inn, Haines Junction, 60°44'N 137°31'W, *P. Caswell PPC-2000-Y-471*, 14 Aug. 2000 (DAO).

This weed of cultivated ground was previously known from Dawson (Cody 1996) and Whitehorse (Cody et al. 2000).

Solidago canadensis L. var. *salebrosa* (Piper) Jones, Canada Goldenrod – YUKON: Slims West Trail, Kluane National Park, 61°00.5'N 138°29'W, *P. Caswell PPC-2000-Y-475*, 22 July 2000 (DAO); dry roadside, Alaska Hwy. west of Yukon River, 60°35.6'N 134°46.8'W, *S. Withers SW00-165*, 7 Aug. 2000 (DAO).

The specimens cited above are the first known from the southwest part of the Territory.

Solidago multiradiata Ait., Northern Goldenrod – YUKON: valley floor, moist shrub/graminoid/moss, Upper Bonnet Plume River Drainage Site #114, 64°24'51"N 132°23'W, *J. Staniforth 00-067*, 6 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory (Cody 1996) of about 115 kilometers southeast of a site adjacent to the Bonnet Plume River.

Sonchus asper (L.) Hill, Spiny Sow-thistle – YUKON: flower bed at Kluane Park Inn, Haines Junction, 60°44'N 137°31'W, *P. Caswell PPC-2000-Y-479*, 13 Aug. 2000 (DAO).

The only site known to Cody (1996) of this introduced weedy species was in the vicinity of Dawson.

Taraxacum lyratum (Ledeb.) DC. – YUKON: convex lower slope, open willow/lichen/moss, Upper Bonnet Plume River Drainage near Site #137, 64°31'57"N 131°32'42"W, *J. Staniforth 00-117*, 9 July 2000 (DAO).

The specimen cited above is an extension of the known range in the Territory of about 190 kilometers east of a site just north of latitude 64°N.

Acknowledgments

We thank Gerald A. Mulligan for the identification of Brassicaceae (Cruciferae) specimens; George Argus for the identification of *Salix* specimens; Stephen J. Darbyshire for the identification of ×*Elyhordeum macounii*, *Elymus elongatus* ssp. *ponticus*, *Elymus junceus* and *Elymus trachycaulus* ssp. *novae-angliae*; Laurie Consaul for the identification of *Puccinellia distans*; Phil Caswell, Jennifer Line, Rhonda Rosie and Stu Withers for their constributions of specimens, many representing very substantial range extensions; Lee Mennell for his excellent drawings; Margaret Cody for assisting the senior author with collections in the summer of 2001 in southern Yukon; Paul Catling for reviewing an earlier version of this manuscript, and especially Leslie Durocher for the many hours inputting this information on her computer.

FIGURE 6. *Hieracium albiflorum* Hook., White Hawkweed (drawn by Lee Mennell).

Literature Cited

Cody, W. J. 1996. Flora of the Yukon Territory. National Research Council (NRC) Press, Ottawa, Ontario, Canada. 643 pages.

Cody, W. J., **C. E. Kennedy**, and **B. Bennett**. 1998. New Records of Vascular Plants in the Yukon Territory. Canadian Field-Naturalist 112: 289-328.

Cody, W. J., **C. E. Kennedy**, and **B. Bennett**. 2000. New Records of Vascular Plants in the Yukon Territory II. Canadian Field-Naturalist 114: 417-443.

Cody, W. J., **C. E. Kennedy**, and **B. Bennett**. 2001. New Records of Vascular Plants in the Yukon Territory III. Canadian Field-Naturalist 115: 301-322.

Cody, W. J., **C. E. Kennedy**, **B. Bennett**, and **V. Loewen**. 2002. New records of Vascular Plants in the Yukon Territory IV. Canadian Field-Naturalist 116: 446-474.

Douglas, G. W., G. W. Argus, H. L. Dickson, and **D. F. Brunton**. 1981. The Rare Vascular Plants of the Yukon. Syllogeus 28: 1-96.

Douglas, G. W., G. B. Straley, D. Meidinger, and **J. Pojar**. 1998. Illustrated Flora of British Columbia, Volume 1 Gymnosperms and Dicotoledons (Aceraceae through Asteraceae). British Columbia Ministry of Environment, Lands and Parks and Ministry of Forests. 436 pages.

Douglas, G. W., G. B. Straley, D. Meidinger, and **J. Pojar**. 1998. Illustrated Flora of British Columbia, Volume 2 Dicotyledons (Balsaminaceae through Cuscutaceae). British Columbia Ministry of Environment, Lands and Parks and Ministry of Forests. 401 pages.

Douglas, G. W., D. Meidinger, and **J. Pojar**. 1999. Illustrated Flora of British Columbia, Volume 3 Dicotyledons (Diapensiaceae through Onograceae). British Columbia Ministry of Environment, Lands and Parks and Ministry of Forests. 423 pages.

Douglas, G. W., D. Meidinger, and **J. Pojar**. 1999. Illustrated Flora of British Columbia, Volume 4 Dicotyledons (Orobanchaceae through Rubiaceae). British Columbia Ministry of Environment, Lands and Parks and Ministry of Forests. 427 pages.

Douglas, G. W., D. Meidinger, and **J. Pojar**. 2000. Illustrated Flora of British Columbia, Volume 5 Dicotyledons (Salicaceae through Zygophyllaceae) and Pteridophytes. British Columbia Ministry of Environment, Lands and Parks and Ministry of Forests. 361 pages.

Douglas, G. W., D. Meidinger, and **J. Pojar**. 2001. Illustrated Flora of British Columbia, Volume 6, Monocotyledons (Acoraceae through Najadaceae). British Columbia Ministry of Environment, Lands and Parks Ministry of Forests. 361 pages.

Douglas, G. W., D. Meidinger, and **J. Pojar**. 2001. Illustrated Flora of British Columbia, Volume 7, Monocotyledons (Orchidaceae through Zosteraceae). British Columbia Ministry of Environment, Lands and Parks Ministry of Forests. 379 pages.

La Frankie, Jr., J. V. 1986. Morphology and Taxonomy of the New World species of *Maianthemum* (Liliaceae). Journal of the Arnold Arboretum 67(4): 371-439.

Porsild, A. E. 1951. Botany of Southeastern Yukon adjacent to the Canol Road. National Museum Bulletin Number 121. 400 pages.

Received 9 October 2002
Accepted 10 October 2003

Notes

Malaxis monophyllos var. *brachypoda*, One-leaved Malaxis, new to the Northwest Territories, Canada

WILLIAM J. CODY[1] and VICTORIA JOHNSTON[2]

[1] National Program on Environmental Health, Agriculture and Agri-Food Canada, Research Branch, Central Experimental Farm, Wm. Saunders Building, Ottawa, Ontario K1A 0C6 Canada
[2] Canadian Wildlife Service, Environment Canada, Yellowknife, Northwest Territories X1A 1E2 Canada

Cody, William J., and Victoria Johnston. 2003. *Malaxis monophyllos* var. *brachypoda*, One-leaved Malaxis, new to the Northwest Territories, Canada. Canadian Field-Naturalist 117(2): 302-303.

The orchid, *Malaxis monophyllos* var. *brachypoda*, is reported from Yellowknife, this being the first record for the Northwest Territories and an extension of about 650 kilometers to the northeast from the nearest population in northern British Columbia.

Key Words: *Malaxis monophyllos* var. *brachypoda*, One-leaved Malaxis, Northwest Territories.

The orchid *Malaxis monophyllos* (L.) Swartz var. *brachypoda* (A. Gray) Morris & Eames (*M. brachypoda* (A. Gray) Fern.) [One-leaved Malaxis] (Figure 1) is known across Canada from Newfoundland and southern Labrador to British Columbia and south in the United States to New Jersey, Pennsylvania, Illinois, Minnesota, Colorado and California. In Canada, it has been considered rare in the provinces of Newfoundland (Bouchard et al. 1991), Nova Scotia (Maher et al. 1978), New Brunswick (Hinds 1983), Manitoba (White and Johnson 1980), Saskatchewan (Maher et al. 1979), Alberta (Packer and Bradley 1984) and British Columbia (Douglas et al. 2002).

On 13 August 2001 the second author observed several plants of One-leaved Malaxis in a Black Spruce swampy area adjacent to the Frame Lake Trail in Yellowknife (62°27'N 114°21'W). One specimen was collected and sent to the senior author for verification and has been deposited in the Agriculture and Agri-food Herbarium (DAO) in Ottawa. This is the first record of this taxon, *Malaxis monophyllos* var. *brachypoda,* from the Northwest Territories. It is an extension of the known range to the northeast of about 650 kilometers from the Liard Hotsprings in northern British Columbia, Mile 396 Alaska Highway, where it was collected by A. F. Szczawinski on 21 July 1961 (DAO). A copy of the map in Porsild and Cody (1980) with the addition of the Yellowknife site is provided (Figure 2). This taxon is an addition to the *Rare Vascular Plants in the Northwest Territories* (McJannet et al. 1995).

The nominate variety of this plant, *Malaxis monophyllos* var. *monophyllos,* is known mainly from Europe but has also been recorded from coastal Alaska. It can be distinguished from var. *brachypoda* by the non-resupinate flowers, the lip being therefore in an uppermost position above the column. In var. *brachypoda* the lip is lowermost due to a twist of 180° in the ovary stalk.

Literature Cited

Bouchard, A., S. Hay, L. Brouillet, M. Jean, and **I. Saucier**. 1991. The rare vascular plants of the island of Newfoundland. Syllogeus 65: 1-165.

Douglas, G. W., D. V. Meidinger, and **Jennifer L. Penny**. 2002. Rare native vascular plants of British Columbia. Second Edition. Ministry of Sustainable Resource Management and Ministry of Forests, Victoria, British Columbia.

Hinds, H. R. 1983. The rare vascular plants of New Brunswick. Syllogeus 50: 1-56.

Maher, R. V., G. W. Argus, V. L. Harms, and **J. H. Hudson**. 1979. The rare vascular plants of Saskatchewan. Syllogeus 20: 1-81.

Maher, R. V., D. J. White, G. W. Argus, and **P. A. Keddy**. 1978. The rare vascular plants of Nova Scotia. Syllogeus 18: 1-37.

McJannet, C. L., G. W. Argus, and **W. J. Cody**. 1995. Rare vascular plants in the Northwest Territories. Syllogeus 73: 1-104.

Packer, J. G., and **C. E. Bradley**. 1984. A checklist of the rare vascular plants in Alberta. Provincial Museum of Alberta National History Occasional Paper Number 5.

Porsild, A. E., and **W. J. Cody**. 1980. Vascular plants of continental Northwest Territories, Canada. National Museum of Natural Sciences, Ottawa, Ontario. 667 pages.

White, D. J., and **K. L. Johnson**. 1980. The rare vascular plants of Manitoba. Syllogeus 27: 1-77.

Received 25 October 2001
Accepted 11 August 2003

FIGURE 1. *Malaxis monophyllos* var. *brachypoda* (drawn by Brenda Carter).

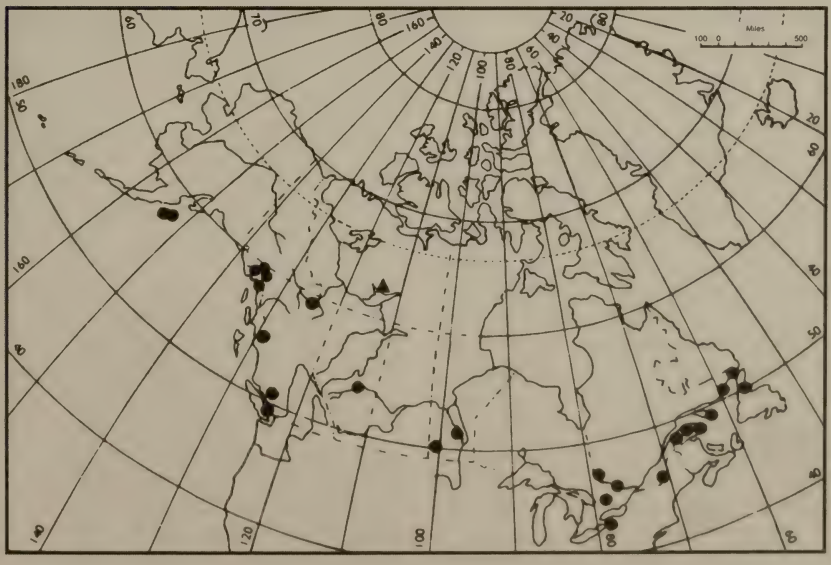


FIGURE 2. *Malaxis monophyllos* var. *brachypoda* from Porsild and Cody (1980) with addition of the Yellowknife site (solid triangle).

An Occurrence of the Hawkweed-Leaved Saxifrage, *Saxifraga hieraciifolia,* in Southern British Columbia, and its Palaeobotanical Implications

STUART A. HARRIS

Department of Geography, University of Calgary, Calgary, Alberta T2N 1N4 Canada

Harris, Stuart A. 2003. An occurrence of the Hawkweed-Leaved Saxifrage, *Saxifraga hieraciifolia*, in southern British Columbia, and its palaeobotanical implications. Canadian Field-Naturalist 117(2): 304-306.

The Hawkweed-Leaved Saxifrage (*Saxifraga hieraciifolia)*, normally found in the alpine tundra in the Arctic, has been collected at 445 m in parkland near Chase, British Columbia. The closest previously recorded occurrence was on the tundra of the Liard Plateau, northern British Columbia. The new occurrence indicates that this species had migrated at least as far south as northern Washington State before the Late Wisconsin glaciation. The latter eliminated the species in British Columbia, but a small population survived south of the glaciers and then, after deglaciation, it migrated north into southern British Columbia, but along the lower limit of the main Boreal Forest instead of above treeline.

Key Words: Hawkweed-Leaved Saxifrage, *Saxifraga hieraciifolia*, distribution, glaciation, disjunct, British Columbia.

Hultén (1968, page 580) shows the distribution of the Hawkweed-Leaved Saxifrage (*Saxifraga hieraciifolia* Waldst. and Kit.) to be circumpolar. More recent additions have been reported for the Northwest Territories and Yukon Territory by Porsild and Cody (1979), Cody (1996), Cody et al. (1998), and W. J. Cody (personal communication). Straley et al. (1985) indicate that it only just enters British Columbia in the northwest at Mount Mansfield and in the northeast on the Liard Plateau at latitude 59° 45'N, 125° 30'W (Figure 1). Douglas, Meidinger, and Penny (2002) and Douglas, Meidinger, and Pojar (2002) also show only these records. All authors consider it to be a species found in moist places on tundra, on alpine meadows, and on soils undergoing solifluction.

While collecting plants at 50° 48' 07.2" N, 119° 44' 20.6" W, on the eastern margin of the Okanagan/ Thompson Plateau, *Saxifraga hieraciifolia* was found as a rare component of the Sagebrush-Ponderosa Pine/ Montane Spruce ecotone (UAC # 69944). The site lies just north of the South Thompson river, west of Chase. The McGillvary Mountain fire stopped some 250 m west of the site in September 2003, so the vegetation is still surviving. The plants were starting to flower on 28 April 2001, amongst Few Flowered Shooting Star (*Dodecatheon pulchellum*) and Glacier Lily (*Erythronium grandiflorum*), and scattered individuals of Yellow Bell (*Fritillaria pudica*) in wet, open areas of the Parkland at an elevation of 445 m. The Hawkweed-Leaved Saxifrage was still flowering in early June, long after the other species were producing seed. This is a vastly different environment to its usual habitat, since it occurs below the Boreal Forest at Chase. The soils are very wet in the Spring due to melting snow. This site also represents a range extension some 8° 57' south of its previously reported most southerly occurrence.

Comparison of these locations with the area glaciated during the Late Wisconsinan event (25 - 11 Ka B.P.) shows that the new southern location is unlikely to have been repopulated from the northern populations in unglaciated portions of the Yukon Territory (Figure 1). Since the icesheets covered all the mountains except for the Outer Queen Charlotte Islands (Calder and Taylor 1968) and the easternmost ranges in southwest Alberta (Harris 1997), they would have destroyed all pre-existing vegetation in their path, and repopulation of the area near Chase is most likely to have occurred by migration from a refugium to the south. A third refugium was suggested by Packer and Vitt (1974) at Mountain Park in the front ranges of Central Alberta, but this has been disproved by Strong (1999). In any case, this is too far from Chase to be a likely source.

This implies that the Hawkweed-Leaved Saxifrage must have spread south along the Cordillera to Washington State prior to the Late Wisconsin ice advance. During the latter, all except a small population at the extreme south of its range as well as in Beringia were wiped out. The southern population would have survived where the unglaciated mountains near the ice margin provided a suitable refugium, though it may not have been at a high elevation. Since Parkland vegetation is very widespread today at most elevations, the saxifrage would not have been limited to tundra environments.

When deglaciation occurred, the tops of the mountains emerged first from the ice, but the Early Holocene climate in British Columbia was dry (Alley 1976; Ryder et al. 1991). Thus suitable wet places that would allow it to migrate northwards would have tended to be at lower elevations where the geology permitted springs to be present, while the refugium in which it had survived the glaciation would have tended to become too dry for its continued survival there. This scenario could explain the disjunct areal distribution of the species, and the change in its habitat to the lower parts of the forested areas.

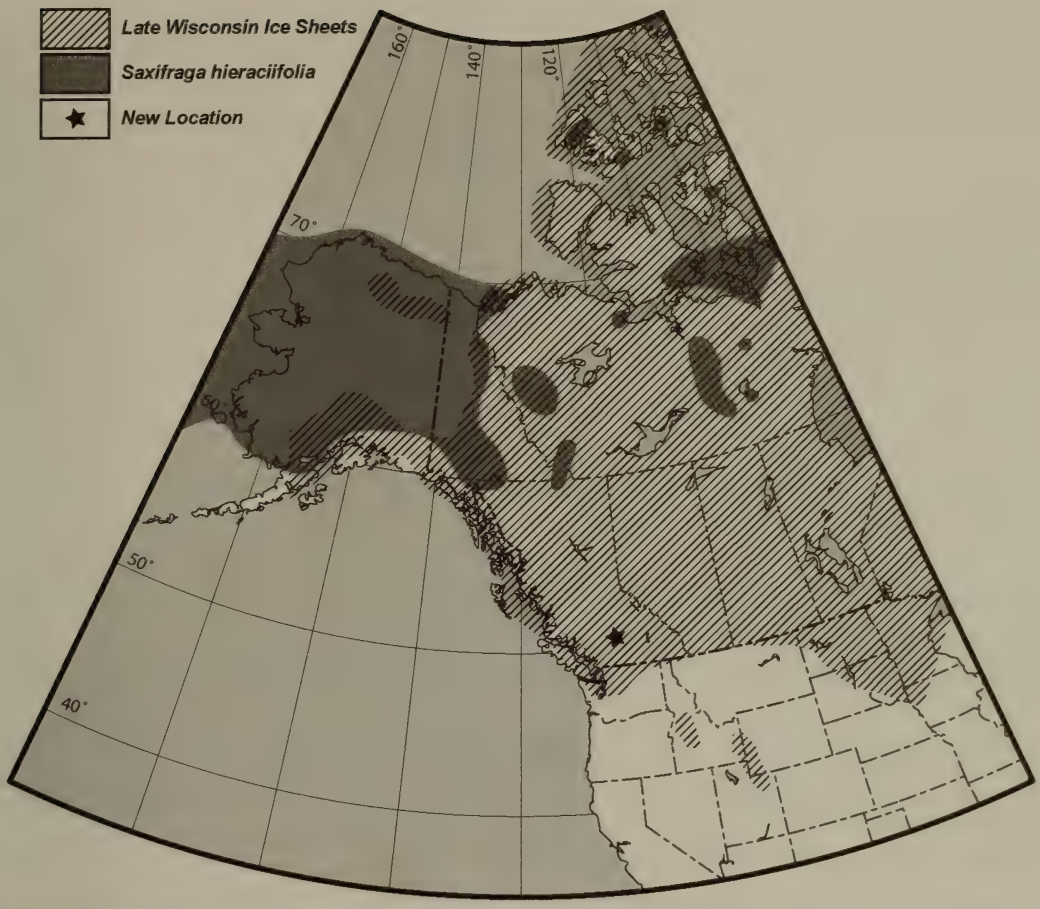


FIGURE 1. Location of the known areas of occurrence of the Hawkweed-Leaved Saxifrage in western Canada in relation to the maximum extent of the Late Wisconsin ice sheets.

In the north, the Hawkweed-Leaved Saxifrage has re-occupied a limited area in northern and southern Yukon, re-colonising it from the population that survived the glaciation in eastern Beringia (i.e., Central Alaska and the western Yukon Territory). In this case, the migration was limited in extent, so that it has only just reached the western margin of the Northwest Territories and northern British Columbia. The isolated pockets to the east in the Northwest Territories presumably survived the ice sheets in local refugia in that region.

Acknowledgements

Thanks are due W. J. Cody, Agriculture Canada, Ottawa, for information and publications, to an anonymous reviewer for hepful suggestions and to Robin Poitras, cartographer, Department of Geography, University of Calgary, for preparation of the map.

Literature Cited

Alley, N. F. 1976. The palynology and paleoclimatic significance of a dated core of Holocene peat, Okanagan Valley, southern British Columbia. Canadian Journal of Earth Sciences 13: 1131-1144.

Calder, J. A., and **R. L. Taylor.** 1968. Flora of the Queen Charlotte Islands, Part I: Systematics of the vascular plants. Research Branch, Department of Agriculture Monograph (4): Part 1. 659 pages.

Cody, W. J. 1996. Flora of the Yukon Territory. National Research Council Press, Ottawa. 643 pages.

Cody, W. J., C. E. Kennedy, and **B. Bennett**. 1998. New records of vascular plants in the Yukon Territory. Canadian Field-Naturalist 112: 289-328.

Douglas, G. W., D. Meidinger, and **J. L. Penny**. 2002. Rare vascular plants of British Columbia. 2nd Edition. Crown Publications, Victoria, B.C. 358 pages.

Douglas, G. W., D. Meidinger, and **J. Pojar**. 2002. Illustrated flora of British Columbia. Volume 8. General Summary, Maps, and Keys. 457 pages.

Harris, S. A. 1997. Relict Late Quaternary permafrost on a former nunatak at Plateau Mountain, S. W. Alberta, Canada. Biuletyn Peryglacjalny (36): 47-63.

Hultén, E. 1968. Flora of Alaska and neighboring Territories. Stanford University Press, Stanford. 1008 pages.

Packer, J. G., and **D. H. Vitt**. 1974. Mountain Park: a plant refugium in the Canadian Rocky Mountains. Canadian Journal of Botany 52: 1393-1409.

Porsild, A. E. , and **W. J. Cody**. 1979. Vascular plants of Continental Northwest Territories, Canada. National Museum of Natural Sciences, Ottawa. 667 pages.

Ryder, J. M., R. J. Fulton, and **J. J. Clague.** 1991. The Cordilleran Ice Sheet and the glacial geomorphology of southern and central British Columbia. Géomorphologie physique et Quaternaire 45: 365-377.

Straley, G. B., R. L. Taylor and **G. W. Douglas**. 1985. The rare vascular plants of British Columbia. Syllogeus (59). 165 pages.

Strong, W. L. 1999. Mountain Park area: a plant refugium in the Canadian Rockies? Journal of Biogeography 26: 413-423.

Received 28 June 2001
Accepted 5 November 2003

A Northern Hawk Owl, *Surnia ulula,* Nest on a Man-made Structure in Alaska

MICHELLE L. REAKOFF[1], JACK L. REAKOFF[1] AND TIM CRAIG[2]

[1]Wiseman, Alaska 99790, USA.
[2]Corresponding author: Northern Field Office, Bureau of Land Management, 1150 University Drive, Fairbanks, Alaska 99708-3844, USA

Reakoff, Michelle L., Jack L. Reakoff, and Tim Craig. 2003. A Northern Hawk Owl, *Surnia ulula*, nest on a man-made structure in Alaska. Canadian Field-Naturalist 117 (2): 306-307.

A Northern Hawk Owl nest was found in a metal cavity on the superstructure of the Trans-Alaska Pipeline. This may be the only record of Northern Hawk Owls nesting on a man-made structure in North America.

Key Words: Northern Hawk Owl, *Surnia ulula,* nesting, man-made substrate.

Northern Hawk Owls (*Surnia ulula)* nest at northern latitudes throughout the boreal forests of the world. Little is known about their nesting ecology when compared with other Strigiformes. The nests recorded in North America have all been in natural cavities in cliffs or trees, cavities in trees that have been excavated by other birds, in old stick nests constructed by other birds, or occasionally, on the limbs of conifers (Bent 1938; Terres 1980; Armstrong 1995; Duncan and Duncan 1998). In addition, Northern Hawk Owls sometimes nest among the dense branches of spruce (*Picea* spp.) that have been parasitized by mistletoe (*Arceuthobium campylopodum*) in northern Alaska (TC, personal observation). Although Northern Hawk Owls are known to nest in nest boxes in Scandinavia (Sonerud et al. 1987; Voous 1989), we have not found a record of this species nesting on man-made substrates in North America.

On 17 April 2000 Alaska Standard Time MLR visited a study plot close to the Trans-Alaska Pipeline via snow machine to collect data on Snowshoe Hare (*Lepus americanus*) foraging behavior. While working at the study site, she heard vocalizations in the nearby spruce forest. These calls continued for about 15 minutes, but she did not see the bird responsible for the sounds. Two days later she returned to the study plot and again heard the same vocalizations. When she had finished her work, she walked along the Pipeline and a Northern Hawk Owl flew from a cavity in part of the steel superstructure that supports the Pipeline. Later that day, she investigated the cavity and found a small nest made of twigs, weed stems, grass and owl feathers. Contained within the nest cup were four small white oval eggs. The nest was located 6 km northeast of Wiseman, Alaska, at 67° 27.68" north latitude and 150° 02.66" west longitude. During these observations snow depth was about 1 m and the temperature was about -2°C.

On 21 April MLR returned to the study plot again, and saw a hawk owl perched in a spruce tree 25 m from the nest cavity. The owl vocalized repeatedly in her presence, using the same call she had heard before. This vocalization was reminiscent of the "Territorial Call" described by Voous (1989) and the "Advertising Call" described by Duncan and Duncan (1998). When MLR drove a snow machine under the Pipeline support structure, a second owl flew from the cavity. She found six eggs in the nest cup. MLR and JLR visited the

nest area again on 24 April and found there were still six eggs in the nest.

On 18 May MLR and JLR visited the nesting area on foot after most of the snow had melted in the area. They observed two adult Northern Hawk Owls. One of the birds was perched in a tree top and vocalized when they approached the Pipeline, the other flushed from the nest cavity when MLR climbed onto JLR's shoulders to investigate the nest. Both adults vocalized and flew from tree-top to tree-top in an agitated manner and one of the adults dove within 1 m of MLR's head during this investigation. Two young and four unhatched eggs were in the nest. In addition, the fresh remains of a Snowshoe Hare lay on the ground beneath the nest. MLR videoed the adults and the nest site during this visit.

We later visited the area and took physical measurements at the nest site. The nest was 2.1 m above the ground, in a cavity that measured about 44 cm tall by 10 cm wide. The cavity was completely open on one side and was 20 cm deep. It was comprised of 1.3 cm thick steel. Near the nest the overstory vegetation has been removed on both sides of the Trans-Alaska Pipeline for a total width of around 20 m. Beyond this cleared area, the overstory vegetation in the vicinity of the nest site was dominated by short (< 7 m) White Spruce (*Picea glauca*). We estimated the canopy coverage of spruce to be < 20% in the vicinity of the nest. Bog Birch (*Betula glandulosa), g*raminoids, and bryophytes covered the ground except near the pipeline. Seasonal and perennial wetlands occurred within 75 m of the nest and the nest site was about 400 m from the Middle Fork Koyukuk River.

In May 2001 and April 2002, we searched the Trans-Alaska Pipeline near the historic nest site but found no Northern Hawk Owls in the area. We located another old nest made of grasses and twigs on a Pipeline support structure immediately next to the nest site. This nest contained a Northern Hawk Owl feather and the amount of bird defecation that coated the sides of the cavity led us to believe that it may have been used by owls in the recent past.

Acknowledgments

Publication of this paper was made possible by the USDI Bureau of Land Management, Northern Field Office. We thank the Alyeska Pipeline Service Company for assistance. Mark Fuller of the USDI Geologic Survey, A. J. Erskine, and David Yokel of the BLM provided helpful comments on the manuscript.

Literature Cited

Armstrong, R. H. 1995. Guide to the birds of Alaska. Alaska Northwest Books, Anchorage. 322 pages.

Bent, A. C. 1938. Life histories of North American birds of prey. U. S. National Museum Bulletin. Number 170. part 2. Washington , D. C.

Duncan, J. R., and **P. A. Duncan**. 1998. Northern Hawk Owl (*Surnia ulula*). *In* The birds of North America. Number 356. *Edited by* A. Poole and F. Gill. The birds of North America, Inc., Philadelphia, Pennsylvania.

Sonerud, G. A., **J. O. Nybo**, **P. E. Fjeld**, and **C. Knoff**. 1987. A case of bigyny in the Hawk Owl *Surnia ulula*: spacing of nests and allocation of male feeding effort. Ornis Fennica 64: 144-148.

Terres, J. K. 1980. The Audubon Society Encyclopedia of North American Birds. Alfred A. Knopf. New York 1109 pages.

Voous, K. H. 1989. Owls of the Northern Hemisphere. MIT Press, Cambridge, Massachusetts.

Received 6 September 2000
Accepted 16 October 2003

Direct Identification of Northern Sage-grouse, *Centrocercus urophasianus*, Nest Predators Using Remote Sensing Cameras

MATTHEW J. HOLLORAN and STANLEY H. ANDERSON

Wyoming Cooperative Fish and Wildlife Research Unit, Box 3166 University Station, University of Wyoming, Laramie, Wyoming 82071 USA

Holloran, Matthew J., and Stanley H. Anderson. 2003. Direct identification of Northern Sage-grouse, *Centrocercus urophasianus*, nest predators using remote sensing cameras. Canadian Field-Naturalist 117(2): 308-310.

The status and apparent decline of Sage-grouse (*Centrocercus* spp.) has been of increasing concern and lower nesting success could be contributing to population declines. Our objective was to directly identify Sage-grouse nest predators. Following visual confirmation of radio-marked Sage-grouse nest establishment in 1997-1999, we installed automatic 35 mm cameras controlled by an active infrared monitor. Of 26 nests monitored by cameras, 22 successfully hatched and four were unsuccessful. American Elk (*Cervus canadensis*), Badger (*Taxidea taxus*), and Black-billed Magpie (*Pica hudsonia*) destroyed three of the four unsuccessful nests, and domestic cattle caused abandonment of the fourth. Richardson's (*Spermophilus richardsonii*) and Thirteen-lined Ground Squirrels (*S. tridecemlineatus*) were recorded at nests, but were not detected in predation.

Key Words: *Centrocercus urophasianus*, Sage-grouse, *Cervus canadensis*, American Elk, ground squirrel, predator.

Northern Sage-grouse (*Centrocercus urophasianus*) were once abundant throughout Wyoming's sagebrush (*Artemisia* spp.) habitats (Patterson 1952). Since the 1970s, however, statewide harvest and lek attendance data indicate Sage-grouse numbers have declined (Wyoming Game and Fish Department [WGFD] harvest reports 1976-1993, Cheyenne, Wyoming; Connelly and Braun 1997). A decline in nesting success has been proposed as a factor contributing to the decline in Sage-grouse populations (Heath et al. 1996*).

Many studies have identified predation as the primary factor directly influencing Sage-grouse nesting success (Batterson and Morse 1948*; Autenrieth 1981*; Crawford et al. 1992*; Heath et al. 1997*). Although most ranchers and hunters consider Coyotes (*Canis latrans*) the primary Sage-grouse predator (Matt Holloran, personal observation), the percentage of bird and eggshell fragments as a whole in Coyote prey base studies ranged from 2 to <7% (Johnson and Hansen 1979; Reichel 1991; Heath et al. 1996*), suggesting minimal impact on Sage-grouse. Common Ravens (*Corvus corax*), Black-billed Magpies, Red Fox (*Vulpes vulpes*), and Badgers (*Taxidea taxus*) have been identified as predominant Sage-grouse nest predators (Autenrieth 1981*; Connelly et al. 1991; Heath et al. 1996*). Patterson (1952) reported that 42% of Sage-grouse nest predation in Wyoming was due to Richardson's and Thirteen-lined ground squirrels (*Spermophilus richardsonii, S. tricemlineatus*).

Predator identification has usually been indirect, based on sign and eggshell characteristics. Our objective was to identify Sage-grouse nest predators directly in the Bates Creek region of central Wyoming.

Methods

Thirty-six female Sage-grouse were captured on and near leks from mid-March through April 1997-1999 on the 31000 ha, high elevation (2170 – 2350 m) Bates Creek Grazing Allotment (42°30'N, 106°15'W) in southeast Natrona County, Wyoming. We used spotlighting and hoop-netting (Giesen et al. 1982; Wakkinen 1990) to capture the grouse. Each hen was fitted with a radio-transmitter package (Advanced Telemetry Systems Inc., Insanti, Minnesota) secured with a PVC-covered wire necklace so the transmitter was on the upper breast. Transmitters weighed 12 g, had a battery life expectancy of 305 days, and were equipped with motion-sensitive sensors. Birds were released at point of capture after processing.

Radio-marked hens were monitored bi-weekly through the pre-laying (April) and nesting (May-June) periods of 1997-1999 using hand-held receivers and 3-element Yagi antennas. Nest locations of radio-marked hens were determined by circling the bird until visual confirmation was made. One week after visual confirmation of nest establishment, we installed an automatic 35 mm camera (TM 35-1™; Trailmastec, Lenexa, Kansas) triggered by an active infrared monitor (TM 1500™; Kucera and Barrett 1993). One camera was placed in a metal ammunition box and concealed in a shrub within 2 m of each nest. We used two cameras in 14 cases where one camera could not cover all major nest visitation routes. The cameras were aligned to capture the activity within the nest bowl and the infrared beams were positioned across the main escape route(s) between five and 10 cm above the ground. The infrared monitor was programmed to trigger the camera when the beam was broken for ≥0.05 seconds, the delay between photographs was 6 seconds (minimums for the equipment), and one picture was taken each time the beam was broken. We used 36-exposure film that was replaced every fifth day. Rubber boots were worn, and sage-masking scent (Wildlife Research Center, Inc., Anoka, Minnesota) was used each time

nests were visited. An additional 12 artificial nests were constructed within randomly determined suitable nesting habitat using either chicken or abandoned Sage-grouse eggs, and monitored until all nests hatched.

Results

Thirty-three of 36 (92%) radio-marked females initiated nests and had camera(s) installed. Seven hens abandoned, possibly as a direct result of camera installment (discussed in Holloran and Anderson, in review). The seven abandoned nests were monitored and included in the sample of 12 artificial nests. Of the 26 Sage-grouse nests with cameras, 22 successfully hatched (85%) and four were unsuccessful. An American Elk, Black-billed Magpie, and Badger predated three of the four unsuccessful nests. Repeated disturbance by domestic cattle (the nest was between an upland pasture and a watering site) caused abandonment of the fourth unsuccessful nest. Additionally, elk were recorded at three artificial nests, and appeared to test the eggs; the eggs were cracked, not eaten. In all four elk involved nest loss cases, bull elk were responsible for eating (the actual Sage-grouse nest) or testing the eggs. Cow elk were recorded at two successful Sage-grouse nests and two artificial sets, but did not show interest in the eggs. Ground squirrels were recorded near three separate nests (two successful, one artificial), but none was destroyed. Other animals recorded at nest sites include: Pronghorn (*Antilocapra americana*), White-footed Mouse (*Peromyscus* sp.), White-tailed Jackrabbit *(Lepus townsendii*), and Least Chipmunk (*Eutamias minimus*). Additionally, badgers were recorded at two artificial nests, but the eggs were eaten at only one of these nests.

Discussion

In the four nest loss cases where elk were involved (the predated nest and the three artificial nests), bull elk were responsible for eating or testing the eggs. Cow elk were recorded at both Sage-grouse and artificial nests, but did not show interest in the eggs. Requirement of calcium and phosphorus of bull elk, which contribute to antler development (Ullrey 1982; Grasman and Hellgren 1993), may have had a role in these predation events. Additionally, Kevin Warner (Boise State University, Boise, Idaho, personal communication) observed Mule Deer (*Odocoileus hemionus*), American Elk, and domestic cows at destroyed artificial songbird nests in Idaho using remote triggered cameras. Red Deer (*Cervus elaphus*) and domestic sheep on the Shetland island of Foula have been documented eating legs and wings of young Arctic Terns (*Sterna paradisaea*), presumably to supplement a calcium-deficient diet (Furness 1988). White-tailed Deer (*O. virginianus*) in Manitoba have been documented eating small birds caught in mist nets, and were suspected in destruction of a Yellow Warbler (*Dendroica petechia*) nest (Sealy 1994).

Thirteen-lined and Richardson's ground squirrels have been indirectly implicated as important Sage-grouse nest predators in Wyoming (Patterson 1952). We recorded both species at active and artificial nests, but the hens did not flush from their nests and no predation was verified. Although ground squirrels have been conclusively identified as predators of waterfowl nests (Sargeant et al. 1998*), our data suggest they do not destroy substantial numbers of Sage-grouse nests.

The Badger at the artificial nest where the eggs were not eaten failed to detect the nest even though it was within 1 m of the eggs. We do not believe this would have been the case had a hen been present, and surmise that increased scent associated with incubation may increase the probability of predation by mammalian predators. Dense, tall herbaceous vegetation may provide scent and visual barriers between the nests of ground-nesting birds and predators, and reduce the probability of predation (Bowman and Harris 1980; Redmond et al. 1982). Therefore, nest site selection and incubation strategies that decrease the amount of scent associated with the nests should increase the probability of hatching success. This hypothesis supports the importance of herbaceous screening cover within Sage-grouse nesting habitat (Gregg et al. 1994; DeLong et al. 1995).

Nest success for our camera-monitored birds was 85%, while typical Sage-grouse nest success estimates are between 40 and 60% (Wakkinen 1990; Connelly et al. 1991; Connelly et al. 1993; Sveum et al. 1998). It is possible that our findings are a function of small sample size (26 nests), the condition of the habitat, or other unknown factors because our results differ from those reported using examination of nests following depredation. Additionally, egg laying and the first third of incubation were not monitored by camera. We suggest that studies of Sage-grouse nesting using photographic techniques be replicated, and we urge caution in interpreting these results without spatial and temporal replication and larger sample sizes.

Acknowledgments

Our gratitude goes to all land owners who allowed access: Mr. and Mrs. Pete Scott, Mr. and Mrs. Charlie Scott, Mr. and Mrs. Jim Price, Mrs. Anne Miles, Mr. and Mrs. Pete Garrott, and Mr. Ron Heward. Brian Heath (WGFD), Todd McCollum, Kevin Downs, Beau Patterson (WGFD), Mike Choma (WGFD), and George Sonne (BLM) provided information and field assistance. The WGFD provided financial support.

Documents Cited (marked * in text)

Autenrieth, R. E. 1981. Sage-grouse management in Idaho. Wildlife Bulletin 9. Idaho Department of Fish and Game, Boise, Idaho.

Batterson, W. M., and **W. B. Morse.** 1948. Oregon Sage-grouse. Oregon Game Commission Fauna Series 1. Portland, Oregon.

Crawford, J. A., M. A. Gregg, M. S. Drut, and **A. K. DeLong.** 1992. Habitat use by female Sage-grouse during the breeding season in Oregon. Final Report. Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon.

Heath, B., R. Straw, S. Anderson, and **J. Lawson.** 1996. Proceedings of the Sage-grouse workshop. 6-7 September 1996, Pinedale, Wyoming.

Heath, B., R. Straw, S. Anderson, and **J. Lawson.** 1997. Sage-grouse productivity, survival, and seasonal habitat use near Farson, Wyoming. Wyoming Game and Fish Department, Completion Report. Cheyenne, Wyoming.

Sargeant, A. B., M. A. Sovada, and **R. J. Greenwood.** 1998. Interpreting evidence of depredation of duck nests in the prairie pothole region. U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, North Dakota.

Literature Cited

Bowman, G. B., and **L. D. Harris.** 1980. Effect of spatial heterogeneity on ground-nest depredation. Journal of Wildlife Management 44: 806-813.

Connelly, J. W., and **C. E. Braun.** 1997. Long-term changes in Sage-grouse (*Centrocercus urophasianus*) populations in western North America. Wildlife Biology 3: 229-234.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, and **K. P. Reese.** 1991. Sage-grouse use of nest sites in southeastern Idaho. Journal of Wildlife Management 55: 521-524.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, K. P. Reese, and **J. W. Fischer.** 1993. Re-nesting by sage-grouse in southeastern Idaho. Condor 94: 1041-1043.

DeLong, A. K., J. A. Crawford, and **D. C. DeLong, Jr.** 1995. Relationships between vegetational structure and predation of artificial Sage-grouse nests. Journal of Wildlife Management 59: 88-92.

Furness, R. W. 1988. Predation on ground-nesting seabirds by island populations of red deer *Cervus elaphus* and sheep *Ovis*. Journal of the Zoological Society of London 216: 565-573.

Giesen, G. L., T. J. Schoenberg, and **C. E. Braun.** 1982. Methods for trapping Sage-grouse in Colorado. Wildlife Society Bulletin 10: 224-231.

Grasman, B. T., and **E. C. Hellgren.** 1993. Phosphorus nutrition in white-tailed deer: nutrient balance, physiological responses, and antler growth. Ecology 74: 2279-2296.

Gregg, M. A., J. A. Crawford, M. S. Drut, and **A. K. DeLong.** 1994. Vegetational cover and predation of Sage-grouse nests in Oregon. Journal of Wildlife Management 58: 162-166.

Johnson, M. K., and **R. M. Hansen.** 1979. Coyote food habits on the Idaho National Engineering Laboratory. Journal of Wildlife Management 43: 951-956.

Kucera, T. E., and **R. H. Barrett.** 1993. The Trailmastec camera system for detecting wildlife. Wildlife Society Bulletin 21: 505-508.

Patterson, R. L. 1952. The Sage-grouse of Wyoming. Sage Books Inc., Denver, Colorado.

Redmond, G. W., D. M. Keppie, and **P. W. Herzog.** 1982. Vegetative structure, concealment, and success at nests of two races of spruce grouse. Canadian Journal of Zoology 60: 670-675.

Reichel. 1991. Relationships among coyote food habits, prey populations, and habitat use. Northwest Science 65: 133-137.

Sealy, S. G. 1994. Observed acts of egg destruction, egg removal, and predation on nests of passerine birds at Delta Marsh, Manitoba. Canadian Field-Naturalist 108: 41-51.

Sveum, C. M., J. A. Crawford, and **W. D. Edge.** 1998. Use and selection of brood-rearing habitat by sage grouse in south-central Washington. Great Basin Naturalist 58: 344-351.

Ullrey, D. E. 1982. Nutrition and antler development in white-tailed deer. Pages 37-48 *in* Antler development in Cervidae. *Edited by* R. D. Brown. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas.

Wakkinen, W. L. 1990. Nest site characteristics and spring-summer movements of migratory Sage-grouse in southeastern Idaho. M. S. thesis, University of Idaho, Moscow, Idaho.

Received 5 March 2001
Accepted 15 July 2003

Autumn and Winter Breeding Records for the American Robin, *Turdus migratorius*

THOMAS GARDALI[1] AND JENNIFER D. WHITE[2]

[1]Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970 USA
[2]Division of Biological Sciences, University of Missouri, 105 Tucker Hall, Columbia, Missouri 65211 USA

Gardali, Thomas, and Jennifer D. White. 2003. Autumn and winter breeding records for the American Robin, *Turdus migratorius*. Canadian Field Naturalist 117(2): 311-312.

We report autumn and winter breeding records for the American Robin (*Turdus migratorius*). We located a nest on the campus of the University of Columbia at Missouri, USA, active 12 to 15 October 1999. This late nesting record prompted us to consult the Cornell Lab of Ornithology's Nest Record Program and Bird Studies Canada's Project NestWatch. Of the 11 113 American Robin nest records in Cornell's database, 15 were active in September and three were active later than September. Of the over 23 000 nest records available from Bird Studies Canada one was active in September and one in October. All four of the latest nests contained nestlings and were active on 3 October 1964 in Massachusetts, 13 October 1932 in Manitoba, 18 November 1964 in West Virginia, and 8 January 1966 in Ohio. Eight of the ten nests monitored until outcome could be determined fledged young successfully.

Key Words: American Robin, *Turdus migratorius*, autumn nesting, winter nesting, Manitoba, Missouri, West Virginia, Ohio.

Recently, the breeding season of the American Robin (*Turdus migratorius*) was defined as going from approximately early April to mid-August with no mention of breeding activity occurring later than August (Sallabanks and James 1999).

On 12 October 1999 we located an active American Robin nest on the campus of the University of Missouri-Columbia, Boone County, Missouri, USA (38° 56' N, 092° 19' W). The nest was placed in a *Magnolia* approximately 2 m from a building. One young fledged on 12 October and a second fledged on 15 October when the nest contained one young. The young robins were being fed the berries of hawthorn shrubs (*Crataegus* sp.), a species commonly cultivated at the University. On 16 October there was no activity at the nest and we found one fledgling dead approximately 20 m from the nest. We believe this late nesting event was not anomalous, because on 12 September 1999 we found two freshly dead robin nestlings (basal 50% of rectrices still ensheathed) under a nest in a residential neighborhood approximately 600 m from the campus.

These observations prompted us to consult the Cornell Lab of Ornithology's Nest Record Program and Bird Studies Canada's Project NestWatch. The Cornell Lab's Nest Record Program contains over 20 000 records for the American Robin of which 11 113 (most before 1984) have been computerized. A search of the computerized records for late dates found 15 September records and three later than September. Nests active in September were from Nebraska (1; 1969), Tennessee (1; 1969), Ohio (1; 1966), Michigan (1; 1971), Illinois (3; 1969, 1970, 1973), Maryland (3; 1965, 1965, 1968), and Alaska (5; all from 1968). Most records in September were of nests apparently late in the nesting cycle with young near fledgling age. However, 3 of the 5 from Alaska were at the egg stage. Three nests from the Cornell database were observed active later than September, 3 October 1964 in Massachusetts, 18 November 1964 in West Virginia, and 8 January 1966 in Ohio; all contained young. A search of approximately 23 000 records available from Québec, Ontario, Manitoba, Saskatchewan, Yukon and Alberta yielded one nest with young active in September (Québec; date not provided) and one nest with young on 13 October 1932 in Manitoba.

Ten nests, including ours, were monitored until outcome could be determined. Of these, eight fledged young, one failed, and one had an uncertain outcome.

Reproductive flexibility in birds is complex and may be influenced by an interaction of environmental factors such as predictive cues (e.g., photoperiod) and supplementary cues (e.g., food supply, temperature; see Hahn et al. 1997 for review). For example, fall breeding has been documented in the Western Scrub-Jay (*Aphelocoma californica*) and Acorn Woodpecker (*Melanerpes formicivorus*) in response to a late acorn crop (Cully 1987; Stanback 1991; Koenig et al. 1995). Fall breeding of the Tricolored Blackbird (*Agelaius tricolor*) has been attributed to an appropriate stimulus, flooding, that occurred out of season (Orians 1960). Fall and winter nesting records for Killdeer (*Charadrius vociferus*) in the southern U.S. were attributed to unusually warm weather over the last decade (Smith et al. 1999).

We have no way of knowing whether the fall and winter breeding records were simply a result of a prolonged breeding season or if breeding had been resumed after completing molt (or both). Additionally, we do not know what factors contributed to the fall and winter breeding records reported here. Conditions with the potential to prolong breeding in the American Robin include mild temperatures and abundant food crops. Urban areas or even individual buildings can produce mild microclimates because concrete streets and buildings may retain or create heat prolonging

warmer temperatures into fall and winter. American Robins are common breeders in urban and suburban areas and all but five of the records described here were classified as either urban or suburban (the five may have been associated with a human setting but location information was insufficient). All of the late records from Alaska, for example, were of nests constructed on or in buildings. Unusually late or abundant food crops may also have the potential to induce or prolong breeding as reported for other taxa. Although we observed robins feeding their young hawthorn berries at the Missouri nest, we do not know if this crop was atypically late or abundant. These data suggest that fall breeding by the American Robin may be regular in some years. Indeed, in Missouri, nests under construction have been observed as late as 18 August (Jacobs and Wilson 1997). Assuming a 13-day incubation period and a 13-day nestling period (Sallabanks and James 1999), a nest under construction on 18 August would fledge around mid-September. Additionally, breeding bird atlases from the Maritime Provinces and Québec report robin nests with young until mid-September (Erskine 1992; Gauthier and Aubry 1996). More study is needed to assess the relationship between breeding season length and reproductive fitness of the American Robin.

American Robins usually complete their prebasic molt by September (Pyle 1997) and in British Columbia gonads of both male and female robins are inactive in July (Kemper and Taylor 1981). It would be interesting to know if the fall and winter breeding robins had completed their prebasic molt and resumed breeding, arrested molt in order to breed, or had not yet initiated molt.

Acknowledgments

We are grateful to James D. Lowe at the Cornell Laboratory of Ornithology for supplying the nest record data. We thank Gavin F. Hanke, Michel Gosselin, Mark Peck, Michael Semenchuk, and Glenn C. Sutter for supplying nest record data from Bird Studies Canada's Project NestWatch. Importantly, we wish to acknowledge the many contributors to the nest record programs. Thanks to Tony Erskine, Steve N. G. Howell, Dana Morris-Porneluzi, and Rex Sallabanks for commenting on early versions of this manuscript. This is Point Reyes Bird Observatory contribution number 1147.

Literature Cited

Cully, J. F. 1987. Autumnal breeding Acorn Woodpeckers in southern New Mexico. Southwestern Naturalist 32: 399.

Erskine, A. J. 1992. Atlas of Breeding Birds of the Maritime Provinces. Nimbus, Nova Scotia Museum (Chelsea Green).

Gauthier, J., and **Y. Aubry.** 1996. The breeding birds of Québec. Canadian Wildlife Service. Environment Canada, Québec Region.

Hahn, T. P., T. Boswell, J. C. Wingfield, and **G. F. Ball.** 1997. Temporal flexibility in avian reproduction: patterns and mechanisms. Current Ornithology 14: 39-80.

Jacobs, B., and **J. D. Wilson.** 1997. Missouri Breeding Bird Atlas, 1986-1992. Missouri Department of Conservation, Jefferson City, Missouri, USA.

Kemper, D. L., and **J. M. Taylor.** 1981. Seasonal reproductive changes in the American Robin *(Turdus migratorius* L.) of the Pacific Northwest. Canadian Journal of Zoology 59: 212-217.

Koenig, W. D., P. B. Stacey, M. T. Stanback, and **R. L. Mumme.** 1995. Acorn Woodpecker (*Melanerpes formicivorus*). *In* The Birds of North America, Number 194. *Edited by* A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C., USA.

Orians, G. H. 1960. Autumnal breeding in the Tricolored Blackbird. Auk 77: 379-398.

Pyle, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, California, USA.

Sallabanks, R., and **F. C. James.** 1999. American Robin (*Turdus migratorius*). *In* The Birds of North America., Number 462. *Edited by* A. Poole and F. Gill. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.

Smith, K. G., W. M. Davis, T. E. Kienzle, W. Post, and **R. W. Chinn.** 1999. Additional records of fall and winter nesting by Killdeer in southern United States. Wilson Bulletin 111: 424-426.

Stanback, M. T. 1991. Autumnal breeding in the Scrub Jay. Journal of Field Ornithology 62: 94-96.

Received 29 May 2002
Accepted 25 August 2003

Observations of Long-tailed Weasel, *Mustela frenata*, Hunting Behavior in Central West Virginia

BRIAN W. SMITH[1], CHRIS A. DOBONY[1], JOHN W. EDWARDS[1], AND W. MARK FORD[2]

[1]Division of Forestry, West Virginia University, PO Box 6125, Morgantown, West Virginia 26506-6125 USA
[2]USDA Forest Service, Northeastern Research Station, PO Box 404, Parsons, West Virginia 26287 USA

Smith, Brian W., Chris A. Dobony, John W. Edwards, and W. Mark Ford. 2003. Observations of Long-Tailed Weasel, *Mustela frenata*, hunting behavior in central West Virginia. Canadian Field Naturalist 117(2): 313-315.

Using infrared video-surveillance systems during 1999–2000, we observed attempts by two individual Long-tailed Weasels (*Mustela frenata*) to depredate female Ruffed Grouse (*Bonasa umbellus*) and their clutch of eggs. Neither female was captured despite Long-tailed Weasel attacks on multiple nights, but all eggs from one nest were either consumed or cached over a two-night period. Although Long-tailed Weasels have been shown to return quickly to areas of abundant prey, return visit behavior to locations where weasels were unsuccessful or only partially successful are poorly described.

Key Words: Ruffed Grouse, *Bonasa umbellus*, Long-tailed Weasel, *Mustela frenata*, nest predation, West Virginia.

Most reports of Long-tailed Weasel feeding behaviors have been anecdotal observations (Criddle and Criddle 1925; Errington 1936; Quick 1944; Mumford 1969; Muths 1998), feeding experiments in a laboratory setting (Quick 1951; Byrne et al. 1978; DeVan 1982), or indirectly inferred from live-trapping and telemetry studies (DeVan 1982). Regardless of method, success rates and specific predatory behavior are lacking for Long-tailed Weasels, especially on ground-nesting birds. Our objective was to document the frequency of Long-tailed Weasel depredation of Ruffed Grouse nests, describe weasel behaviors recorded at the nest, and determine the outcomes of any visit by weasels to these nests.

Study and Methods

Our study was conducted at the Mead-Westvaco Wildlife and Ecosystem Research Forest (MWERF) located in Randolph County, West Virginia (38°44' N, 79°58' W) from 1999–2000. Mead-Westvaco established the MWERF (3413 ha) in 1994 to study the impacts of industrial forestry on Appalachian ecosystems and ecological processes. Located in the unglaciated Allegheny Mountain and Plateau physiographic province, elevations range from 740 m to 1200 m. Most of the MWERF contained 60–80 year-old second-growth stands that have been subjected to repeated diameter-limit harvests over the past two decades. A detailed description of the study area is provided in Dobony (2000).

During the nesting seasons (mid-April to early June) of 1999-2000, we used miniature infrared video cameras and time-lapse video recorder systems (Fuhrman Microcam2 camera + Fieldcam LCTLV time-lapse video recorder, Fuhrman Diversified, Seabrook, Texas) to monitor Ruffed Grouse nests (1999: $n = 9$; 2000: $n = 11$). Our video systems recorded continuously over 24 h using standard T-160 videocassettes, but at 3:1 ratios of real time to video time (i.e., an 8 h videocassette recorded 24 = h of activity). Cameras recorded black-and-white images and emitted infrared light at 950 nm, a wavelength not visible to vertebrate species (R. Fuhrman, Fuhrman Diversified, Inc., personal communication). Video cameras, including integrated infrared emitters, were housed within a $32 \times 32 \times 60$ mm aluminum casing. Cameras were attached to an articulating clamp-arm that was used to secure them to substrate near nests. Cameras were mounted within 1 m of nests because infrared emitters only had an effective range of ≤1 m. We equipped each camera housing and articulating clamp-arm with a cloth camouflage sleeve, and we mounted cameras in the most inconspicuous locations possible. Connected by cable, the time-lapse recording system and a 12-volt battery (power source) were hidden from view 20 m from nests.

We changed batteries and videocassettes at each nest daily. We examined each videocassette upon return from the study area to check nest status (i.e., depredation, incubation, or hatched) or if any animals other than Ruffed Grouse had visited the nest during the 24-h period. If a depredation or visitation had occurred, we further analyzed videocassettes to reveal the identity of the predator or visitor, time and duration of visit, and outcome of the visit. Herein, we restrict our discussion to events involving Long-tailed Weasels.

Results

We recorded Long-tailed Weasels at two of 20 (10%) video-monitored Ruffed Grouse nests: one in 1999 and one in 2000. In both years, Long-tailed Weasels visited each nest twice, with visits occurring on consecutive evenings/nights. Videotaped Long-tailed Weasels were not individually marked, and we were unable to determine if more than one individual weasel was involved in consecutive visits at each nest, or the sex of those observed. However, Long-tailed Weasels are known to sometimes return to potential food sources (DeVan 1982), and we assumed that the same individual weasel made consecutive visits to each Ruffed Grouse nest. Because annual survival of weasels is low (Fagerstone 1987) and the nests visited were farther apart (>5 km) than typical for a Long-tailed Wea-

sel home range (DeVan 1982), it is unlikely the same weasel visited both grouse nests across both years.

In 1999, Ruffed Grouse female 151.503 (identified by radio-frequency) began incubating 12 eggs on 25 April. On 2 May, a Long-tailed Weasel attempted to prey upon this female at 01:49:00. The Long-tailed Weasel initially was seen walking on a downed log directly above (approximately 0.3 m) the grouse, which remained motionless on the nest. After a brief pause, the Long-tailed Weasel jumped from the log onto the grouse's back. The female escaped the attack and moved just out of the camera's view. The Long-tailed Weasel remained at the nest bowl for a brief period, smelling the eggs within the nest and feathers surrounding the nest. The Ruffed Grouse occasionally could be seen trying to harass the Long-tailed Weasel away from the nest. The Long-tailed Weasel left the camera's view at 01:49:39 without taking eggs or further attempting to capture the nearby grouse.

On 3 May 1999, female 151.503's nest was visited again by a Long-tailed Weasel. The Long-tailed Weasel initially appeared at 03:43:46 and jumped from the downed log towards the grouse's head. Again, the grouse was able to escape attack by flushing from the nest. The Long-tailed Weasel subsequently smelled the eggs in the nest and then left the camera's view. This visit lasted only 8 seconds.

Female 151.503's nest was depredated on 20 May 1999; unfortunately, the camera had been removed on 18 May for another aspect of the study. Sign at the nest indicated that the marauder was a mammalian predator, but it was impossible to narrow it down to a particular species (i.e., nest appeared to have been visited by several species after depredation and all eggs were missing with only a few egg shell fragments remaining).

In 2000, Ruffed Grouse female 151.172 initiated incubation of 11 eggs around 2 May, and a video system was placed at her nest on 6 May. On 18 May, BWS (senior author) approached the area at approximately 08:00:00 to change the battery and videotape. A Ruffed Grouse flushed from the general location of the nest (females rarely, if ever, flushed from a nest upon approach to change equipment), indicating some other disturbance. Upon investigation through binoculars, BWS saw that the nest had been disturbed, finding seven eggs displaced approximately 4 m downhill. Six eggs were still intact and one had cracked upon impact with a rock. BWS could not find eggshell fragments or other signs of predation near the nest. BWS returned the six intact eggs to the nest to determine if the Ruffed Grouse or the predator would return to the nest for the remaining eggs.

When the videotape from 17/18 May was reviewed, it showed that a Long-tailed Weasel attempted to capture the grouse at 01:14:03 on 18 May. The Long-tailed Weasel initially was seen walking on a portion of exposed tree root-wad directly above (approximately 0.2 m) the grouse, which remained motionless on the nest. The Long-tailed Weasel then leapt from the root toward the female. Female 151.172 appeared to fly away from the immediate area. The Long-tailed Weasel remained at the nest bowl, smelling eggs and feathers within the nest. It then began to smell the eggs actively, rolling seven of them out of the nest bowl with its nose. The Long-tailed Weasel finally consumed the contents of one egg on video, after several unsuccessful attempts at opening the egg. In doing so, the Long-tailed Weasel curled into a tight ball (lying on its side) while holding the egg with all four feet. The Long-tailed Weasel proceeded to rotate the egg until the egg apex was in its mouth. It eventually punctured the eggshell and began lapping the contents of the egg through the hole created in the egg's top. The remaining three eggs were moved to an area outside the camera's view; it is unknown whether these eggs were consumed or cached. The Long-tailed Weasel left the camera's view at 01:27:39.

On 18 May 2000, after we replaced the six eggs, presumably the same Long-tailed Weasel returned to the nest (although the grouse never returned). At 17:02:25, the Long-tailed Weasel entered the nest and proceeded to remove three eggs from the nest bowl and away from the camera's view. The Long-tailed Weasel left the camera's view for the final time at 17:11:19. The following day, we found two eggs cached under a root stem and leaves approximately 10 cm from the nest bowl. Another egg was cached under a downed log approximately 0.5 m from the nest. Its contents had been consumed.

Discussion

Given the disparity in body sizes (80–250 g for female Long-tailed Weasels and 160–450 g for males [Fagerstone 1987], and 450–650 g for female Ruffed Grouse [Rusch et al. 2000]), it is surprising that this small mustelid would attempt to capture an adult Ruffed Grouse. However, Long-tailed Weasels are rather opportunistic and generalized in their dietary habits and have been known to prey on animals larger than themselves (e.g., Cottontails [*Sylvilagus* sp.] and Snowshoe Hares [*Lepus americanus*]; Fagerstone 1987). Of particular interest in our findings was the difference between the outcomes of the attempted depredations; one Long-tailed Weasel appeared only interested in capturing the grouse, leaving the eggs unmolested whereas the other consumed or cached many of the eggs after failing to capture the nesting female. Unfortunately, we were unable to determine what type of mammalian predator returned to destroy female 151.503's nest.

Ground-nesting birds and their eggs are thought to compose only a small portion of Long-tailed Weasel diets (Fagerstone 1987). For example, 11% of destroyed Blue-winged Teal (*Anas discors*) nests were depredated by weasels (Teer 1964), only 12% of fecal

samples in Iowa contained feathers or egg fragments (Errington 1936), and in only two of four areas where weasel diets were sampled were avian remains found in fecal samples (Simms 1979). Bump et al. (1947) reported that approximately 11% (49 of 463) of Ruffed Grouse nests were destroyed by weasels but believed this was probably a conservative estimate because another 40 (9%) depredated nests were attributed to either weasel or fox.

Despite how infrequently avian remains appear in Long-tailed Weasel diets, our videography shows that they can be very disruptive to ground-nesting birds. Continual flushing of an incubating bird, regardless of whether the Long-tailed Weasel captures the bird or removes any eggs, likely has a negative impact on survival of the young. Moreover, extended absence from the nest can expose eggs to excessive cooling or other predators. In addition to the egg caching we captured on video, we have witnessed entire Ruffed Grouse broods lost to predation in a 24 h period. At least one was very suggestive of Long-tailed Weasel predation (Dobony 2000, B. Smith, unpublished data). Therefore, it appears that Long-tailed Weasels can be considered potential predators (direct effects) and nest disrupters (indirect effects) of Ruffed Grouse and thus potentially could be influencing Ruffed Grouse productivity in the Appalachian Mountain region. Ruffed Grouse densities are lower in the southern portion of its range than in more northern reaches (Bump et al. 1947), potentially because of lower productivity at southern latitudes (Bergerud 1988). Dobony et al. (2001) reported nest depredation to be a primary factor influencing Ruffed Grouse nest success in West Virginia.

Acknowledgments

Our study was conducted as part of the Appalachian Cooperative Grouse Research Project and was supported in part by West Virginia Division of Natural Resources (Pittman-Robertson Federal Aid in Wildlife Restoration Project W-48-R) and the Division of Forestry, West Virginia University. We thank the Richard King Mellon Foundation and The Ruffed Grouse Society for additional funding, Mead-Westvaco Corporation for logistical support, and the West Virginia Cooperative Fish and Wildlife Research Unit for use of their video surveillance systems. Additionally, we thank T. Allen, N. Herbert, J. Johnson, T. Olexa, and S. Sutton for assistance with field work.

Literature Cited

Bergerud, A. T. 1988. Mating systems in grouse. Pages 439–472 *in* Adaptive strategies and population ecology of northern grouse. *Edited by* A. T. Bergerud and M. W. Gratson. University of Minnesota Press, Minneapolis.

Bump, G., R. W. Darrow, F. C. Edminster, and **W. F. Crissey**. 1947. The ruffed grouse: life history, propagation, management. New York State Conservation Department. 915 pages.

Byrne, A., L. L. Stebbins, and **L. Delude**. 1978. A new killing technique of the long-tailed weasel. Acta Theriologica 23: 127–131.

Criddle, N., and **S. Criddle**. 1925. The weasels of southern Manitoba. The Canadian Field-Naturalist 39: 142–148.

DeVan, R. 1982. The ecology and life history of the long-tailed weasel (*Mustela frenata*). Dissertation, University of Cincinnati, Cincinnati, Ohio, USA. 300 pages.

Dobony, C. A. 2000. Factors influencing ruffed grouse productivity and chick survival in West Virginia. M.S. thesis, West Virginia University, Morgantown. 97 pages.

Dobony, C. A., J. W. Edwards, W. M. Ford, and **T. J. Allen**. 2001. Nesting success of ruffed grouse in West Virginia. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 55: 456–465.

Errington, P. L. 1936. Food habits of a weasel family. Journal of Mammalogy 17: 406–407.

Fagerstone, K. A. 1987. Black-footed ferret, long-tailed weasel, short-tailed weasel, and least weasel. Pages 549–573 *in* Wild furbearer management and conservation in North America. *Edited by* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch. Ontario Trappers Association, North Bay, Ontario, Canada.

Mumford, R. E. 1969. Long-tailed weasel preys on big brown bats. Journal of Mammalogy 50: 360.

Muths, E. 1998. An observation on caching of prey by a long-tailed weasel (*Mustela frenata*). The Southwestern Naturalist 43: 106.

Quick, H. F. 1951. Notes on the ecology of weasels in Gunnison County, Colorado. Journal of Mammalogy 32: 281–290.

Rusch, D. H., S. DeStefano, M. C. Reynolds, and **D. Lauten**. 2000. Ruffed grouse (*Bonasa umbellus*). *In* The Birds of North America (515). *Edited by* A. Poole and F. Gill. The Birds of North America, Inc., Philadelphia, Pennsylvania.

Simms, D. A. 1979. North American weasels: resource utilization and distribution. Canadian Journal of Zoology 57: 504–520.

Teer, J. G. 1964. Predation by long-tailed weasels on eggs of blue-winged teal. Journal of Wildlife Management 28: 404–406.

Received 21 June 2002
Accepted 5 November 2003

Aggressive Interactions of Rocky Mountain Elk, *Cervus elaphus nelsoni*, During the Calving Season Toward Mule Deer, *Odocoileus hemionus*, in Central Colorado

ROBERT M. STEPHENS[1], A. WILLIAM ALLDREDGE[2], AND GREGORY E. PHILLIPS[3]

[1]Wyoming Game and Fish Department, 528 South Adams Street, Laramie, Wyoming 82070 USA
[2]2518 Owl Creek Road, Thermopolis, Wyoming 82443 USA
[3]EDM International, Inc., 4001 Automation Way, Fort Collins, Colorado 80525 USA

Stephens, Robert M., A. William Alldredge, and Georgy E. Phillips. 2003. Aggressive interactions of Rocky Mountain Elk, *Cervus elaphus nelsoni*, during the calving season toward Mule Deer, *Odocoileus hemionus*, in central Colorado. Canadian Field-Naturalist 117(2): 316–317.

We documented four aggressive interactions between Rocky Mountain Elk (*Cervus elaphus*) and Mule Deer (*Odocoileus hemionus*) during the Elk calving season of June and July 1995. In one case, we believe a fawn Mule Deer was killed by two cow Elk. In the other three cases, Elk chased Mule Deer away from an area where they were grazing. These incidents are of interest because documentation of such interactions between Elk and Mule Deer is sparse in the scientific literature and because of the concern about declining Mule Deer populations throughout the western United States.

Key Words: Rocky Mountain Elk, *Cervus elaphus nelsoni*, Mule Deer, *Odocoileus hemionus*, competition, attack, aggression, interaction.

Aggressive interactions between Rocky Mountain Elk (*Cervus elaphus nelsoni*) and Mule Deer (*Odocoileus hemionus*) are not well documented in scientific literature. Elk and Mule Deer appear compatible in most areas, and are frequently observed feeding in close proximity (White 1958; Hirsch 1963). When Elk become concentrated, however, Mule Deer may leave the immediate area. In northern Idaho, Mule Deer use of major salt licks decreased as Elk use increased (Young and Robinette 1939). Waldrip (1977) reported that White-tailed Deer (*Odocoileus virginianus*) appeared to avoid Elk and were not regularly seen in areas containing dense Elk populations. Telfer and Cairns (1986) reported that groups of cow Elk with calves "mob" solitary Moose (*Alces alces*), eventually forcing the moose to leave the area. Aggressive behavior by Elk towards deer has been documented in confinement, where a White-tailed Deer immobilized with succinylchlorine chloride collapsed and an Elk (one of seven) rushed over and struck the deer roughly with its front feet (Scanlon 1977). We know of only one other incident where cow Elk were observed striking and killing a fawn Mule Deer (F. Lindzey, personal communication).

We witnessed four aggressive interactions between Elk and Mule Deer. The first was on Meadow Mountain (39°35'N, 106°28W) in the White River National Forest, Eagle County, Colorado on 22 June 1995. The meadow where the observation occurred was approximately 1.5 km × 0.75 km. Observations were made with 10 × 40 binoculars at 200 – 300 m. The first animal to enter the meadow that evening was a female Mule Deer. She was alert and scanned the meadow for nearly 5 minutes before she began to feed. About 10 minutes later, 10 Elk (7 cows, 2 calves and 1 bull) entered the meadow. While the Elk fed they encountered a bedded Mule Deer fawn close to the forest edge. Two cows chased the fawn for approximately 100 m until it reached the timber and escaped. The Elk returned to the meadow within a few minutes and continued to graze. Near the middle of the meadow they encountered a second bedded fawn. Seven female Elk and two calves chased the fawn for nearly 100 m for about 10 seconds. The fawn screamed several distress cries while running, and then sought shelter under a small shrub. Two female Elk aggressively stomped on the fawn with their front hooves and the fawn appeared limp after several blows. We inspected the location the following morning, but found only hair from the fawn and a trampled shrub. Thus, we were unable to conclude the fawn's fate, although we believe it was killed. We did not inspect the area until the following morning because our work required repeated observations of Elk in this meadow (Phillips and Alldredge 2000) and our disturbance would have compromised that work.

We observed two other aggressive interactions between Elk and Mule Deer on Meadow Mountain and a third at McCoy Park (39°35N, 106°32W), also in the White River National Forest in Eagle County, Colorado. On 7 July 1995, 22 Elk (18 cows, 4 calves and 0 bulls) were grazing and using a mineral lick at Meadow Mountain. Two female and one male Mule Deer approached the mineral lick when two Elk chased them away. On 8 July 1995, two female Mule Deer were chased from the same mineral lick by a single Elk (1 of 38 with at least 5 calves in the herd). Lastly, on 23 July 1995, we observed a female, a calf, and two yearling male Elk chase a male Mule Deer from the area they were grazing in McCoy Park.

As Mule Deer populations throughout much of the West appear to be declining and Elk populations are thought to be increasing, some have speculated that interspecific competition may be a causative factor (Lindzey et al. 1997). Our observations certainly suggest that Elk will displace Mule Deer. Our observations occurred during the calving and calf-rearing season (June and July), suggesting Elk might be particularly aggressive toward other animals they perceive as threats to their offspring during this period.

Acknowledgments

We are grateful to Vail Associates, Inc. for funding our research on the effects of human disturbance to Elk calf survival. Bill Andree, Colorado Division of Wildlife, provided invaluable assistance throughout the three years of our study.

Literature Cited

Hirsh, J. B. 1963. Range use, relationship to logging, and food habits of the elk in the Little Belt Mountains, Montana. Master's thesis, Montana State University, Bozeman, Montana. 44 pages.

Lindzey, F. G., W. G. Hepworth, T. A. Mattson, and **A. F. Reese.** 1997. Potential of competitive interactions between mule deer and elk in the Western United States and Canada: A review. Wyoming Cooperative Fisheries and Wildlife Research Unit, Laramie, Wyoming. 82 pages.

Phillips, G. E., and **A. W. Alldredge.** 2000. Reproductive success of elk following disturbance by humans during calving season. Journal of Wildlife Management 64: 521-531.

Scanlon, P. F., R. E. Mirarchi, and **J. A. Wesson.** 1977. Aggression toward immobilized white-tailed deer by other deer and elk. Wildlife Society Bulletin 5: 193-194.

Telfer, E. S., and **A. L. Cairns.** 1986. Resource use by moose versus sympatric deer, wapiti and bison. Alces 22: 113-137.

Waldrip, G. P. 1977. Elk habitat use during calving season with possible effects on white-tailed deer at the Wichita Mountains National Wildlife Refuge. M.S. thesis, Oklahoma State University, Stillwater, Oklahoma. 81 pages.

White, K. L. 1958. Summer range ecology of Rattlesnake Creek mule deer in the spruce-fir zone. Master's thesis, The University of Montana, Missoula, Montana. 95 pages.

Young, V. A., and **W. L. Robinette.** 1939. Study of the range habits of elk on the Selway Game Preserve. Bulletin 34. University of Idaho, Moscow, Idaho. 47 pages.

Received 11 March 2002
Accepted 17 November 2003

Book Reviews

ZOOLOGY

Trout and Salmon of North America

By Robert J. Behnke, illustrated by Joseph R. Tomelleri. 2002. The Free Press, Simon and Schuster Inc., New York. viii + 360 pp., illus. U.S. $44.10.

This book describes the trouts and salmons of North America, comprising the genus *Oncorhynchus* with 9 species and 25 subspecies, the genus *Salmo* with 2 species (one, the Brown Trout, introduced), and the genus *Salvelinus* with 5 species and perhaps 5 subspecies. It also includes the Arctic Grayling and Mountain Whitefish as "other salmonids". The latter two species are not the sum total of other salmonids in North America so their inclusion seems a little arbitrary.

The book begins with introductory sections on origins and evolution, classification and taxonomy, life history and biology, and morphology and anatomy. There is an epilogue (about the author's life and the genesis and track of his interest in salmonid fishes), an artist's note (about methods used in drawing the fishes for the book), acknowledgements, a species list, a selected bibliography, a glossary, and an index. However 329 pages are devoted to the fish in a book with dimensions of 25.5 cm wide by 23.5 cm high, ideally suited to displaying the fish drawings in a full page spread. Several drawings showing spawning and non-spawning individuals, and sea-run and resident fish are depicted for some species. The colour pencil drawings were made from nature, based on a preserved specimen after photographing it freshly caught and taking colour notes. These drawings are a very attractive feature of the book and were made into a 2003 calendar sold separately and doubtless to be sold in subsequent years as demand from anglers and naturalists will most probably be high.

Each species account comprises one to several colour illustrations, a colour distribution map, a short introductory section, a description of the species, a sidebar with the scientific, common and other names, habitat, length and weight (American and metric units), life span and diet, and sections on biology, distribution, evolution and classification, and conservation. The text is interesting and easy to read. Occasionally there are sections within each species account devoted to a particular problem or point of interest. A Canadian example is the giant Gerrard Kamloops Trout (*Oncorhynchus mykiss*) one of which attained 24 kg when stocked in Jewel Lake, British Columbia, where forage fish were an abundant food resource. Giants like this are no longer seen.

The maps comprise colour-shaded ranges. They are easy to understand and for the localized subspecies are narrowly defined. Spot distributions are not given and would perhaps have been revealing of literature and museum specimen records in light of deduced maximum ranges and in assessing rarity of modern captures if a time element had been incorporated.

The taxa described in this book are a mix of generally accepted species, long established, and the author's own interpretations based on a lifetime's study of these fishes. In the latter category in particular, he recognizes 3 North American subspecies for the Arctic Char, 11 subspecies for the Rainbow Trout, and 14 subspecies for the Cutthroat Trout, some or all of which may be open to different interpretations by other authors. Not all have been named scientifically and many are endangered by habitat loss and genetic swamping by introductions of related stocks or species and a few are now extinct. Authors and dates for the species are not given anywhere in the book, a curious omission for a taxonomic based study but perhaps a recognition of Eschmeyer's *Catalog of Fishes*, so readily available on-line.

The author notes that his studies on salmon and trout began in 1957 and, without wishing to belabour the point, this will soon be a 50-year stretch of time. Despite the internet, published papers are still the original source for information on ichthyofaunas and on taxa. It takes time and money to accumulate these and, in taxonomic studies, none can be ignored if hard to find or in other languages. The cost of accumulating such material and, if necessary translating it, is very high and is often spread over many years. A full understanding of North American trout and salmon cannot be undertaken without considering the literature on Russian populations, for example. With this in mind authors who produce career-summarising works such as this, need to state that their collection of papers, data and specimens have been or will be deposited at an institution or at least provide a bibliography on-line or as a CD with the book. The bibliography in the book is short and meant only as an entry point to the literature.

The book lacks habitat photographs which could usefully have shown the diverse range of environments that these fishes are found in. There are no identification keys in the classic sense although for species these are available in other works and subspecies and unnamed taxa are mostly defined by distribution in isolated drainage basins. Identification is by means of a small colour drawing of a fish, sometimes of only a

spawning adult, sometimes of both sea-run and stream-resident forms, with enlarged details of key colour features. This does not allow all life stages to be identified and obviously would not work on preserved material. Tabulated comparisons of characters for the numerous subspecies would have been a useful addition to the book.

The Index is somewhat incomplete in that scientific names occur only in full – to find *aguabonita* you would have to be aware that it occurs under *Oncorhynchus mykiss* (in older literature it was known as *Salmo aguabonita*).

This book is a fascinating read and an indictment of management practices for native fishes. It should be of great interest to naturalists, anglers, and conservationists. For scientists studying these or any other fishes it is an examplar of a particular taxonomic point of view and well worth consideration.

BRIAN W. COAD

Canadian Museum of Nature, P. O. Box 3443, Station D, Ottawa, Ontario K1P 6P4 Canada

Bigelow and Schroeder's Fishes of the Gulf of Maine

Edited by Bruce B. Collette and Grace Klein-MacPhee. 2002. Smithsonian Institution Press, Washington and London. Third Edition. xxxiv + 748 pp., illus. U.S. $75.

This volume is a revised edition of an earlier work, originally published in 1925 and re-worked in 1953. The latter has long been a standard reference work, as recognized in this new edition by the authors' names in the title, and of great value to Canadians on the Atlantic coast interested in fish and fisheries. The new edition was 13 years in the making and has 38 contributors, including the editors, an indication of the volume of knowledge and the consequent increasing specialisation of scientists.

The layout follows the pattern of other books on fishes, with a Foreword, Preface, Acknowledgements, Acronyms and Abbreviations (useful for the neophyte and the forgetful), Contributors, and a 7-page History of the Fishes (actually the fisheries). The species accounts follow, arranged by families in systematic order, then there are 39 distribution maps, a comprehensive 107 pages of Literature Cited, and Indices of scientific and common names. The species accounts are preceded by a general description of the family, of varying length and depth of treatment. The area of coverage includes parts of New Brunswick and Nova Scotia.

The Contents serves as a checklist for the 252 species in 118 families covered by this book, 33 species more than the 1953 version.

Species accounts comprise common and scientific names, other common names, page of the account in Bigelow and Schroeder (1953), and an illustration. Text headings may vary within each account but can include Description, Meristics, Color, Size, Distinctions, Habits, Food, Feeding by Larval and Juvenile Stages, Feeding Behavior, Predators, Parasites, Reproduction, Spawning Season, Spawning Behavior, Early Life History, Age and Growth, Larval and Juvenile Distribution, Larval and Juvenile Habits, General Range, Occurrence in the Gulf of Maine, Migrations and Movements, Importance, Stocks, and Management, among others. Not all species have entries under all these headings as some, for example, do not migrate or do not have commercially important stocks. Some accounts are quite short, less than a page, while the Atlantic Herring, for example, runs to 16 pages.

Common names are capitalized above the illustration at the beginning of each species account but not in the text. Traditionally fish common names are not capitalized, unlike those of birds and certain other groups, but arguments have been advanced to start this (Nelson et al., 2002). Certainly Atlantic Cods would clearly mean more than one individual *Gadus morhua* while Atlantic cods could mean several different cod species found together in the Atlantic Ocean.

Minor errors are inevitable in a work of this length with numerous authors, e.g. Labrador is misspelled on page 665, but the most serious one is the orientation of illustrations of right-eyed flatfishes. Convention has it that fish illustrations have the head on the left but this does not work with these flatfishes. Their left eye "migrates" during development so that both eyes are on the right side of the fish. Their "belly", bottom or blind side is actually their left side, not the ventral surface. To view the uppermost, pigmented and eyed side of these fishes, the head must be on the right. The illustrations have been mirror-imaged in this book and represent a body form that does not exist (note that the families of left-eyed flatfishes correctly have images with their heads on the left; and that some right-eyed species very rarely have left-eyed individuals).

There is no key to families, often a useful way of narrowing down possibilities for those new to an ichthyofauna. There is a key to Percoidei, the largest suborder of perch-like fishes but this again presupposes some knowledge of fish classification. The keys to species within families do not give the page number of the description so a lot of page turning is needed to locate the species account in speciose families; luckily most families have relatively few species. In addition the keys give the common name and the species are arranged alphabetically by scientific

name. Even more confusing is the key to sculpins so-named (actually the superfamily Cottoidea) which includes the single member of the poachers (Agonidae) , a fathead sculpin (Psychrolutidae) and a sea raven (Hemitripteridae) as well as the sculpins (Cottidae).

The systematic treatment is very up-to-date and careful delving can reveal new records for Canadian waters where the Gulf of Maine overlaps into New Brunswick and Nova Scotia. Occasionally some points may be questioned – why is *Scomberesox saurus saurus* listed as a trinomial? Another subspecies exists but its distribution is not in the area under consideration.

The end plates give an overview of the geography of the Gulf of Maine but omit some salient features. There is no border between the USA and Canada in the sea, Halifax is not marked but is mentioned in illustrations and capture localities, and such places as Georges Basin are referred to in the text but not indicated.

Canadian scientists will need to refer to this volume as it corrects identifications in Scott and Scott's (1988) *Atlantic Fishes of Canada*. It also provides a review of work done on many species since the mid-1980s and on the changes that continue to occur in the northwest Atlantic fish populations – Atlantic Cod are no longer "Canada's single most important commercial species", for example.

This book gives a thorough treatment of the biology and systematics of these fishes, many of them familiar to residents of maritime Canada, and is a most significant addition to our knowledge of North American fishes.

Literature Cited

Nelson, J. S., W. C. Starnes, and **M. L. Warren**. 2002. A capital case for common names of species of fishes – a white crappie or a White Crappie. Fisheries 27(7):31-33.

BRIAN W. COAD

Canadian Museum of Nature, Box 3443, Station D, Ottawa, Ontario K1P 6P Canada

A Spring Expedition to the Falkland Islands and Antarctica

By Diantha L. Knott. 2002. Masalavita Video Productions, Oregon. 55 minutes VHS Video U.S. $30 + $5 Shipping.

This is a video of an early summer (November, the equivalent to June in the north) voyage of 2000 plus miles to the Antarctic area at the south end of the Atlantic Ocean. The video covers the Falkland Islands and the Antarctic Peninsula, but not South Georgia and the South Orkneys or the Pacific side of Antarctica. The tape comes with two photocopies of maps showing the itinerary.

The video quality and photography are very good. The images are crisp and have a good depth of field. The colours are true. The sound is well balanced and clear. The narrator's voice is gentle and relaxing, but not soporific. There is no musical background. Instead the sea and wind fill the spaces between the limited, often simplistic, narration.

The video covers most of the major Antarctic species of bird and mammal. I counted about two dozen named species of bird and five species of mammal. The two species of Antarctic flowering plants were not mentioned. This is a good introduction to this region for the potential eco-traveller. The main characters are the five species of penguin. These birds are natural actors and the footage will be a great delight to penguin fans. With the other birds and mammals covered, this video gives a great sense of this remote region. The rocks, ice, scenery, colours, and weather are artistically portrayed and provide the viewer with a good understanding of the land and wildlife. Also, the videographer has included some footage of life on a cruise. Shots of people landing, walking, eating, and frolicking are included. I estimated this occupied about 15% of the film and thought some of these scenes were too long (two minutes of watching people eat at a BBQ was 1.75 minutes too long!).

The ardent naturalist may be somewhat more frustrated. A number of birds included in this film were not identified (e.g., White-chinned Petrel, Grey-headed Albatross). Some others were only given a generic identification (e.g. shag, skua) and some that were mentioned were not seen (e.g., the storm petrels). Some identifications are delayed for up to several minutes (most notably with Adelie Penguins). Overall, I think about 40 bird species is a reasonable tally for such a cruise, with perhaps a few more on a good trip. Most noticeably there were several "standard" birds that were completely missing (Royal and Wandering Albatross over the ocean, Turkey Vultures in the Falklands). The narrator does not give any information on abundance. As the footage on the Southern Fulmar is less than that of an Antarctic Petrel a viewer might infer that fulmars are the rarer species. As the itinerary goes through the breeding area of the fulmar, they will be abundant. In contrast, the petrel breeds at some distance from the peninsula and are likely to occur in very small numbers.

I thought that a dozen species of mammal are more likely to be seen than the five depicted in the video. Especially missing were the whales; only a Killer Whale from the pod north of the Lemaire Channel is shown. The narrator does not mention the common species (Minke, Humpback) or the dolphins and does

not differentiate the species of fur seals. There are three mentions of Weddel Seal. The first does not look like a Weddel and the second time implies the Weddels and Elephant seals consort and call together. They do not and the footage shows only Elephants. The first shot of a Crabeater Seal is not identified while a later one is shown as the "first" sighting.

There are some comments on the historical significance of some sites, but these are not made in any context. For example, during the footage on Elephant Island the narrator comments on Shackleton's experience. It is left to the viewer to know or find out about Shackleton's expedition. Similarly the hut at Hope Bay (near the Esperanza Research Base) is identified only as Swedish from 1902. It is one of three huts from the Swedish South Polar Expedition led by Otto Nordenskjold. The base of another hut (on Paulet Island) is shown, but not identified. It was built by the survivors of the wrecked vessel "Antarctic" under Captain C. A. Larsen, who were also members of the Swedish South Polar Expedition.

Visitors must remember that this is a springtime movie and some of the bird distributions will change noticeably as the season advances. Also the snow and ice cover will be diminished by January–February. However, whenever you go, you should see all of the species depicted within the same general area. This is a very good video for people who plan to visit or have visited this area. It gives an excellent sense of the stark but fascinating nature of this unforgiving wild land and its inhabitants. The footage of the penguins alone is quite delightful.

ROY JOHN

2193 Emard Crescent, Beacon Hill North, Ottawa, Ontario K1J 6K5 Canada

Shorebirds of the Yellow Sea: Importance, Threats and Conservation Status

By M. A. Barter. 2002. Wetlands International Global Series 9, International Wader Studies 12, Canberra, Australia. 104 pp. Available free on internet, www.wetlands.org, 2.5 Mbt Word or 3.5 Mbt pdf.

This book is done and supported by individuals who went way beyond the horizon and came back with fame and appreciation; they just followed the birds. The East Asian Australasian Flyway (EAAF) is gigantic. This flyway not only presents tongue-breaking location names, it also connects the Australian and Asian wintering grounds with the breeding grounds in the Russian Arctic and even Alaska. Many of the huge mudflats with their shorebirds are still unkown and await their investigation. Australia and its well-known shorebird enthusiasts ("shorebird-aholics") present the powerful "engine" to further such investigations on shorebirds along the EAAF. These individuals set a great example to be followed worldwide. Besides its unique and endemic birds, this flyway also offers great opportunities to evaluate findings from flyways elsewhere in the world. The author summarizes efficiently in 9 chapters over 10 years of field work in the Yellow Sea. This region presents over 36 shorebird species and is a key location for the EAAF during the migration and non-breeding seasons. Each of the 36 species is described well in the Species Accounts, which provide the international audience with official flyway estimates, important coastal regions of occurrences and many other details such as counting results for the migration seasons and literature references. In addition, a description (e.g., area, coordinates, protection status, threats, etc.) is given for 27 of the most relevant shorebird migration sites in the Yellow Sea, known to date. Two chapters are devoted to shorebird threats, and conservation of shorebirds and their habitat. This topic cannot be emphasized strongly enough since the Yellow Sea harbours not only a high biodiversity but also globally threatened species such as the Spotted Greenshank (*Tringa guttifer*) and Spoon-billed Sandpiper (*Eurynorhynchus pygmeus*), as well as near-threatened species like Eastern Curlew (*Numenius madagascarensis)* and Asian Dowitcher (*Limnodromus semipalmatus)*. For six of the shorebird species the region carries, during northward migration, almost the entire breeding population of the flyway.

The text of this technical publication is written very well and efficiently, and the tables and black-and-white maps serve their purpose nicely. Summaries of the text in Korean and Chinese are provided, too. One should keep in mind that 12 major Asian rivers drain into the Yellow Sea; plenty of mudflats and estuaries to survey. Therefore, the publication raises the issue of how to survey migratory shorebirds efficiently in quantitative terms and for such a huge area? This book provides first answers, but leaves also some topics unanswered. For instance, how big is the underestimation of shorebirds at specific sites due to high turn-over rates? How many species get overlooked; e.g., for the rare birds such as Spoon-billed Sandpiper and Spotted Greenshanks (with an estimated global population of 1000 individuals). Predictive Modelling of shorebird populations and abundance still awaits its application. Birds need habitat, and the author outlines well which conservation policies work best to protect and

conserve (migratory) shorebirds in the Yellow Sea region. At least the classical concepts might not work well, and RAMSAR agreements and other full-blown international political tool boxes are weak and soft; e.g., due to lack of enforcements and binding. Of interest is the progressive coastal ecoregion approach presented in Chapter 7, which allows one to characterise shorebird habitat with a variety of multidisciplinary habitat data. Much more of such work is needed in order to provide quantified results for shorebirds as well as their habitat.

Although major countries like China, North and South Korea are currently not well known for their efforts to conserve shorebirds and their habitat, this publication will hopefully help to improve the current situation and force the governments eventually to take (coastal) environment issues seriously. The author can be congratulated for his tremendous effort providing the international community with such a splendid report on shorebird conservation and crucial baseline data.

FALK HUETTMANN

Department of Geography–Earth Science, Calgary University, 2500 University Drive N.W., Calgary, Alberta T2N 1N4 Canada
Present address: Biology and Wildlife Department, Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775-700 USA

Birds of the World: A Checklist

By James F. Clements. 2000. Ibis Publishing Company, Vista, California. 867 pp.

Let's be clear about one thing, this is not a field checklist. It's a massive, door-stopping tome. But what a tome it is: all serious birders and ornithologists will want to own their own copy of this long-awaited and authoritative work. For over a decade successive editions of "Clements" have been the authority when it comes to questions on what counts, and what doesn't: the American Birding Association has long used it as its global listing standard. The latest edition will not disappoint.

The bulk of the book consists of a comprehensive listing of all the species of birds of the world. Species names and taxonomy largely follow decisions of the American Ornithologists Union and the British Ornithologists Union; where the author varies from this appropriate references are provided. Each entry has the English name of the species in bold print, followed by the Latin name in italics. In a major improvement over earlier editions, this is followed by a listing of all acknowledged subspecies, albeit in Latin only. This is an exceedingly useful feature, particularly given the pace of taxonomic change in which today's subspecies could be tomorrow's species. Beside each subspecies entry is a short description of its global range. Each species has a handy tick box for those hard-core listers out there and a space to enter information on your own sightings. That's it; no text, no photos, no maps.

There is a short introduction, a helpful list of abbreviations ("Tas." stands for Tasmania), another helpful list of orders and families, and a shamefully long list of extinct species (almost all from islands). There is also a list of major family references for those who want to get into the details or argue about specific decisions, as well as an extensive bibliography. A gazetteer provides geographic reference points for places cited in the text. Listers – and biogeographers – will find the lists of endemic bird species by country, and the distribution of bird species by country, highly useful. Rounding out the picture are separate indices of scientific and English names. The front piece has a colourful map showing the distribution of bird species by country, the end piece a similar map showing endemic species, also by country.

The approach taken by Clements is unflinchingly anchored in the biological species concept; a species is considered valid when it is reproductively isolated. This is in contrast to a phylogenic approach which looks for clusters of shared characteristics. This may disappoint some, as is the decision to not recognize as discrete species many insular forms. Nonetheless, the number of recognized species has exploded from 8600 to 9700, largely based on increased knowledge, including the growing use of DNA analysis. Few global travellers will fail to see their bird list grow by a careful analysis of the revised listing, and many Canadian subspecies have been elevated to full species.

One of the most exciting aspects of this work is its evergreen character; inevitably a book of this nature is out of date almost as soon as it is published. To counter this the author has made it a living work by periodically posting updates to the publisher's web page: serious birders will add "www.ibispub.com" to their internet bookmarks and visit regularly to keep track of the latest lumps and splits. At the time this review was written there have been several updates. For example, in December, 2002, American Herring Gull, *Larus smithsonianus,* was elevated to full species level. Not surprisingly, there is also a software companion (at an extra cost) to help you keep track of sightings electronically, and the "Clements" list is already the standard in competing software out there.

Are there flaws? It would be impossible for a few not to creep in, and a careful perusal will quickly turn up several, starting on page one, where the line to enter your comments is missing for Northern Cassowary. Also, and despite being a great birding destination, Jamaica has "only" 27 endemics, not the 200-300 one

might assume from the end piece. Bird rich Bolivia somehow was left out of both the country summaries. Range descriptions are inconsistent, for example, for Laysan Albatross we learn that it breeds on various islands but also that it "ranges n Pacific", whereas for Black-footed Albatross we learn only where it breeds. Similarly, Lesser Black-backed Gull, surely a fixture of the North American avifauna, is noted only for the old world. Introductions go unnoted, thus there is no indication that House Sparrow occurs in North America. While the list of extinct species is already long enough, it is perhaps optimistic to omit from it Sunda Lapwing, unrecorded from heavily populated and well-watched Java for over eighty years. On a somewhat related note, the decision to drop the symbol in earlier editions indicating that a species is "red listed" by the World Conservation Union/IUCN was unfortunate.

These flaws are largely inconsequential; however, there are also errors in the taxonomy. Many of these are being picked up in the periodic updates and the web page encourages readers to report any errors that they find. One egregious Canadian example is the Sharp-tailed Sparrow complex where *subvirgatus* and *alterus* are listed as Saltmarsh Sharp-tailed Sparrow *caudacutus*, as opposed to Nelson's, *nelsoni*, neatly adding James Bay to the former species' breeding range. Despite these flaws, if you are a serious ornithologist, an avid global birder, or need a one-stop reference which lists every species and subspecies of bird on the planet, this book is for you.

MARK GAWN

1354 Viking Drive, Ottawa, Ontario, K1V 7J6 Canada

The Rockfishes of the Northeast Pacific

By Milton S. Love, Mary Yoklavich, and Lyman Thorsteinson with contributions from John Butler. 2002. University of California Press, Berkeley. x + 405 pp. Cloth U.S.$ 92.95, paper U.S.$ 26.95.

There are a least 65 species of rockfishes (family Sebastidae) in the northeast Pacific Ocean from Mexico to Alaska including about 38 from British Columbia (my count from maps in this book and other sources, the book lists 30-35 species and its maps 31-35). It describes 2 species not given in Hart (1973) nor in Coad et al. (1995) for Canada, namely *Sebastes melanostomus* and *S. rufus*. Rockfishes are important and sometimes dominant components of the marine ecosystem, may live as long as 205 years, have been sought for food and sport, and populations are in severe decline.

The book comprises a series of introductory chapters covering the biology of rockfishes, their evolution, their names, and their fisheries. The biology sections cover habitats, reproduction, ecology of pelagic young, juvenile settlement, movements and activity patterns, age and growth, parasites, abnormalities and diseases, fisheries, and conservation. These are followed by a key to species, species accounts (169 pages), references (34 pages), locality maps, 8 appendices, a glossary, an index, and lists of reviewers, personal contributors, contributing authors, photographers, and artists.

The species accounts comprise scientific name, official common names (as recommended by the American Fisheries Society Committee on Names of Fishes), etymology, colloquial names, a distribution map, description of the fish as it appears underwater and after capture, particularly important for deepwater species that appear very different once hauled to the surface, maximum size, range both geographic and depth, life history, fishery, remarks, and references. Remarks include taxonomic comments but also life history data are not included in that section, which seems an unnecessary separation of information.

The book has a number of strengths. There is an extensive list of references, several underwater colour photographs of most species that effectively convey the variation in these colourful fishes, comments in the species descriptions of similar species and how to differentiate them, and appendices listing such items as parasites, growth and length-weight curves, meristic characters, and the infamous head spines through which these species are often identified. Some art work is unnecessary (see below) but the gyotakus (fish prints from fresh specimens) are very beautiful and add to the argument that "rockfishes are cool".

One criticism is that the drawing of head spine configurations is the same drawing for each species – the absence of a line from a label name to a spine indicates that spine is absent. This is not intuitively easy to follow or visualize on a fish specimen at hand. Another point needing improvement is the distribution maps. These show the species range as a yellow band along the Pacific coast. The text must be read to find any limitations on this simplistic mapping. Spot distribution maps would better indicate the scientific knowledge, backed by museum specimens, on distribution.

The keys have not been tested by me but as a museum scientist it would fall apart for me at couplet 4 where colour alone is used to separate two lines of identification (and the key goes on for 70 couplets, quite long and therefore easy to lose your way). The authors do admit that the key works best on newly caught fish, may not work with juveniles and will prove frustrating on preserved fish. Some effort could have been made to assuage the museum scientist, perhaps

by making local keys where fewer species are involved or expanding on such observations as longspine thornyheads have "branchiostegals usually with scales" – how frequent is usually? The compilation of countable characters is simply a list of pectoral, anal and dorsal fin rays, gill rakers, lateral line pores, and vertebrae. It might be possible to analyse these as a combination of characters that can be used to key out fish or at least unequivocally narrow the choices where species diversity is high.

Most books of serious scientific bent are devoid of humour, rightly so in the judgment of some. This book is eccentric in that its strong scientific and highly technical content is interspersed with humorous asides. These will not be to the taste of all but certainly enliven the book. We learn on page 1 that the genus of rockfishes, *Sebastes* meaning "magnificent", was coined by Baron Cuvier who was blessed with a whole series of Christian names and then adopted his late brother's name but, being "ordered, austere, disciplined, and pompous" was unlikely to have been called "Georgie", "Nikky" or "Cuvie" by his contemporaries (this is merely silly); on page 10 Theodore Gill is captioned as "grouchy and sowed confusion in his wake" in respect of rockfish taxonomy (too harsh?); Figure 7.4 on declining annual recruitment of juvenile bocaccio is a line graph in the best scientific tradition but has the young rockfish spilling out of a baby carriage (drives the point home but quaint); the gap between the two cultures of science and art is no better illustrated than on page 46 where a painting of a man with a rockfish swallowing/biting the top of his head is captioned "Fish Head" (no explanation for the poor scientist); and on the last page the blurb about the senior author states that he is "A quick-tempered man of huge ego, we would not cross him if we were you" (a joke by his co-authors or a cause for concern to reviewers?).

This book is an essential, if quirky in parts, guide for anyone interested in rockfishes or their biology in the northeastern Pacific.

Literature Cited

Coad, B. W., with H. Waszczuk, and I. Labignan. 1995. Encyclopedia of Canadian Fishes. Canadian Museum of Nature, Ottawa and Canadian Sportfishing Productions, Waterdown, Ontario. viii + 928 pages, 128 colour plates.

Hart, J. L. 1973. Pacific Fishes of Canada. Bulletin of the Fisheries Research Board of Canada, 180: ix + 740 pages.

BRIAN W. COAD

Canadian Museum of Nature, P. O. Box 3443, Station D, Ottawa, Ontario K1P 6P4 Canada

Caviar: The Strange History and Uncertain Future of the World's Most Coveted Delicacy

By Inga Saffron. 2002. Broadway Books, New York. xv + 270 pp. U.S.$ 35.95.

There has been a recent trend to popular books on individual fish species, such as cod and shad, and now we have reached the *reductio ad absurdum* of a book on fish eggs. But these eggs form caviar, an economically important and status-rich commodity whose bearers are now facing extinction from overfishing, habitat loss, and pollution. True caviar comes from members of the sturgeon family Acipenseridae and this book details the biology and fisheries of these giant fishes in North America and, after the collapse of fisheries there, in the Caspian Sea. An idea of the value of caviar can be gained from the cost of beluga caviar in Heathrow Airport where it climbed from £76 for a 50 g tin in December 1993 to £208 in November 2000 (personal observations). A single sturgeon has produced 360 kg of caviar worth, on the above prices $3.74 million today, although such monster fish are never seen now and caviar weights are well under 100 kg and mostly less than 50 kg.

The author is a journalist who was in Russia at the time when concern over the loss of the Caspian Sea sturgeons became a popular item in newspapers and magazines although it had long been known by biologists that their survival was threatened. Her lack of biological knowledge is apparent in the text and a few examples can be cited here. She considers that "According to all the usual rules of evolution, the sturgeon should be extinct already" because of their long reproductive cycle (the differences between r- and k-selection are not understood). She also has the powerful tail swooshing food towards its mouth on page 31, refers on page 32 to the *Acipenser* order (rather than genus), has the beluga (*Huso huso*) listed as *Husa husa* and the Kura River as the Kuro on the only map, has sturgeons hatching in one day on page 36, has baited hooks for sturgeons as useless on page 50 (for an interesting read on catching Canadian sturgeons on hook-and-line see Glavin (1994)), and has the sturgeon's front fins enabling the fish to speed through the water (rather than used for steering).

So while the biology in this book must be taken with a pinch of salt, just like caviar, the politics of the resource and the human failings around its management are the core of the book and a fascinating and salutary read. Perhaps one of the most curious conclusions of this book is that state-controlled fisheries in such diverse systems as those of the Soviets and the

Islamic Republic of Iran best conserved the sturgeon stocks while laissez-faire capitalism in America and in post-Communist Russia completely failed these fishes. Most sturgeons are now considered in imminent danger of extinction and some are probably only maintained by hatchery stock.

The caviar industry in former Soviet waters of the Caspian Sea is detailed along with modern skullduggery. The caviar industry in Iran is less well covered and the historical mischief there has not been investigated by the author. Apparently the fisheries in Iran were first granted by the government to Stepan Martinovitch Lianozoff, an Armenian subject of Czarist Russia in the 1870s, regularly renewed. In 1896 the lease was renewed at an annual cost of 450,000 gold francs. In one version of events, Martin (the grandson of Stepan) disappeared in 1923, kidnapped while meeting two ravishing Armenian sisters, leaving only a letter ceding his rights in the caviar fishery to the Soviets. Another version simply has Martin selling his rights to the Soviet Government.

There is a longish review of the origin of the word caviar, based apparently on one man's quest to prove it is Greek. However the word caviar may come from the Farsi "chav-jar" meaning "a cake of strength or power" or "bread of lovers" in allusion to its reputed aphrodisiac qualities; havyar in Turkish means "fish eggs" but this may be of more recent derivation.

The procedures for catching sturgeons, for extracting and processing their eggs as caviar is well described. The bodies were often simply discarded, but some sturgeons have also been utilised for their flesh and the author waxes lyrical on her personal experience of the taste. Simply cooked stellate sturgeon, however, can be execrable (at Bandar Shah on the Iranian shore from my experience).

Perhaps the most disappointing aspect of this book is its lack of illustrations. Sturgeon, their fisheries and habitats, caviar, and the caviar-processing factories are all good photographic subjects and are readily available. The author paints some excellent word pictures, for example in her depiction of the now lost town of Caviar, USA, but it is always fascinating to compare the word and the figure.

The book is a compelling read for anyone interested in the loss of a great and renewable natural resource and an instructive guide to the failings and successes of political systems when attempting to manage species of great value.

Literature Cited

Glavin, T. 1994. A Ghost in the Water. New Star Books, Vancouver. 78 pages.

BRIAN W. COAD

Canadian Museum of Nature, P. O. Box 3443, Station D, Ottawa, Ontario K1P 6P4 Canada

Resource Selection by Animals

By B. J. Manly, L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Kluwer Academic Publishers, Dordrecht. 221 pp. U.S. $78.00.

This second book of papers recently presented at the First International Conference on Resource Selection by Animals in Laramie, Wyoming is truly a bible for wildlife researchers. The authors present Resource Selection Functions (RSF) as a unified theory for the study of resource selections and how to quantify them.

The focus of this book is the statistical aspects of resource selection as relevant for any Wildlife and Fisheries Biologists. This key publication defines "resources" as food and habitat. Much confusion exists in the wildlife literature about use, selection and preference of habitat and food, but the authors provide brilliant clarification: "Selection is the process in which an animal chooses a resource, and preference is the likelihood that a resource will be selected if offered on an equal basis with others (Johnson 1980)". Addressing habitat preferences is the key to managing wildlife habitats efficiently. Obviously, one can only derive preference when resource availability is known; a topic of debate. "However, if we learn there is selection for or against a resource then this is a starting point for further in depth study". This is a drawback for spatial applications of RSFs since they deal mostly with pure abundances; e.g., presence/absence or densities. Although a first step to knowing resource preferences, a pure abundance view can be misleading and, as the authors note, it can only be a basis for more in-depth studies. RSFs likely should also address fitness and relevant ecological processes; topics of future research.

The general RSF concept is actually quite old, and its first application dates back as early as the 1920s by A. Scott. The first edition of this book was published in 1993, but the updated second edition also includes such advanced topics such as AIC, GIS, Risk Assessment, Alternative Modelling Methods, Discrete Choice Models and spatial species predictions. Personally, I find that this new version is much more readable than the previous one.

All important RSF sampling design issues are addressed: Sampling Protocols A, B and C, and Design I (Populations), II (Individuals) or III (each Animal). Also, all assumptions for using RSFs successfully are

explained. "The availability of various resources is not generally uniform in nature, and use may change as availability changes". This is particularly true when the scale of the study changes; therefore, multiscale RSFs are recommended.

Ultimately, almost any radio-telemetry study will apply RSFs sooner or later. The beauty of RSFs is that they can be used for such a huge variety of applications; most of them deal with wildlife species, but the book also shows an example that deals with pre-historic site preferences of Maya settlements. There is almost nothing to stop the RSF concept being used for botany.

This nicely structured book is divided into 14 chapters, a summary and exercises. A full list of symbols is given, which facilitates the understanding of the terminology and formulas greatly. The book also presents some RSF computing advice; e.g., short SAS software codes. In addition, the wildlife biologist will also appreciate the seven pages of RSF-references, and the many examples that deal with classical wildlife studies, for instance the ones by Neu et al. 1974 (Moose habitat selection), Ryder 1983 (Pronghorn wintering habitat), Harris 1986 (Fernbird nest site selection), Popham 1944 (Minnows foraging on Corixids) and Bartunock et al. 1976 (animals depleting their prey). Further, sample datasets are also presented (but not in digital format).

The book is also very strong in presenting all common indices of selectivity. RSFs can be used to assess old-fashioned HSI (Habitat Suitability Index) and Habitat Capability mapping and even to quantify ecological wildlife niches. As the experienced authors state, it is hoped that RSFs replace less powerful ad hoc methods.

Most of the authors of this book are affiliated with Western EcoSystems Technology Inc., a well known environmental NGO (non-governmental organization) in Cheyenne, Wyoming, which sets world standards when it comes to RSFs. The authors make clear that most RSFs are correlational *per se*. Specifically RSF-GIS studies are exploratory, pointing towards new hypothesis and field studies. The GIS chapters are very timely, readable and will be appreciated by the scholar, although this chapter is relatively slim. The use of "spatial bins" and Remote Sensing imagery is shown, but for instance the use of aspect is not explained nor is how to correct for terrain slope underestimations in 2-dimensional GIS mapping. Another topic not fully addressed is statistical model selection when many predictors are involved; e.g., as commonly encountered in modern GIS studies; the Burnham and Anderson (2002) reference is still required. Another good set of additional references to keep in mind is the ones dealing with DISTANCE Sampling, e.g. Buckland et al. (2001), to derive absolute abundances (densities). Many RSF applications rely on high quality wildlife survey data.

In times of literally "exploding" data availabilities; e.g., via the WWW, the reviewer is personally convinced that Neural Networks will play a major role on the future RSF field; and the authors give credit to these and to other algorithms and approaches such as Compositional Analysis and Mahalanobis Distance. Applications of jackknifing and bootstrapping are shown as well. Despite the extremely good coverage for RSFs in this book, Resource Selection Probability Functions (RSPFs) are less well described. Color graphs are not given, but therefore this "bible" is affordable. It is really impressive to read the sections on how RSFs can be used for Spatial Predictions, Risk Assessment of Future Actions and Population Viability Analysis; e.g., Boyce and McDonald (1999).

This book presents well-structured and sound information for the advanced, as well as for the general wildlife biologist. It is a reference on "how to". Some people suggested that this book has an index problem as the latter is only two pages long and has mis-matching page numbers. However, this should not hold back anyone from reading this book. It is simply a must for any wildlife biologist and conservationist. Without RSFs, efficient research and conservation of wildlife and habitat resources is impossible. It is hoped that this brilliant book will aid safeguarding these resources.

FALK HUETTMANN

Geography Department-Earth Science, 2500 University Drive N.W., University of Calgary, Calgary, Alberta T2N 1N4 Canada

All-Weather Hawk Watcher's Field Journal

By Donald Heintzelman. J. L. Darling Corporation, Tacoma, Washington. 66 pp.

This handy pocket field notebook, 12 by 17.5 cm., consists of a conservation note, a one-page introduction, a three-page list of the diurnal birds of prey of North and Central America, and 51 pages for field observations. At the top of each page are blanks to fill in for date, time, weather, and location, including GPS coordinates. The special feature is the use of all-weather writing paper so that one can write in the rain!

C. STUART HOUSTON

863 University Drive, Saskatoon, Saskatchewan S7N 0J8 Canada

Firefly Encyclopedia of Reptiles and Amphibians

Edited by Tim Halliday and Kraig Adler. 2002. Firefly Books, Willowdale, Ontario. 240 pp., Illus. $40

All of the world's more than 13 000 species of amphibians and reptiles are profiled in this clearly written and wonderfully illustrated book. Well, not every species is mentioned, but every family and representative species from each family are portrayed.

The book is divided into two main parts, with the first half of the book dedicated to amphibians and the second half to reptiles. Each part begins with an introductory essay discussing the biology of the group as a whole. A series of brief (1-2 pages) essays then covers key issues. The amphibian section includes essays on taxonomy, metamorphosis, parental strategies, amphibian decline, and conservation. The reptile section features essays on dinosaurs, thermoregulation, conservation, and temperature dependent sex determination. Following these essays there are sections of various lengths on each of the main taxonomic groups (generally orders). For amphibians there are features on caecilians (unfortunately only 4 pages in length), salamanders, and anurans. The reptile part has sections on turtles, lizards, worm-lizards, snakes, tuatara, and crocodilians. Many of these sections feature other short essays on key topics. For example, there are essays on salamander courtship, the Asian turtle crisis, lizard adaptations to deserts, and snake bites.

Within every section there are profiles of each of the families. Each profile provides handy tidbits on each of the families including a map of the global distribution of the family, the number of species and genera, a list of representative species, range of size within the family, as well as the number of species which are globally at risk. The book concludes with a detailed glossary and bibliography.

In order to have the most up to date information Halliday and Adler have solicited contributions from 36 experts on various topics and species groups. While most of the contributors are from the USA there are experts from a total of 7 different countries. This brings a greater depth of knowledge about the subjects in general, but occasionally results in minor contradictions. For example, on page 27 we correctly learn that female Mudpuppies guard their eggs, while on page 52 it is stated that the male guards the eggs.

The book is also profusely illustrated with exceptional colour photos on almost every page. The editors should also be commended for their use of colour illustrations. For example, pages 48-49 illustrate 12 different species of salamanders from 7 of the 10 families. The grouping of so many species together brilliantly displays the diversity of form and colour within salamanders.

There are a few minor things to gripe about: while the editors are generally good about providing both common and scientific names, they don't always do this. The editors have also adopted an odd habitat of only capitalizing the first word of common names of species. They do this whether it is a proper noun or not. And occasionally they don't capitalize any part of the common name. They also sometimes switch back and forth from the species name (e.g. Eastern Newt) to the subspecies name (e.g. Red-spotted Newt). These are minor quibbles when considering the daunting task of summing up the global knowledge on such diverse life forms. Overall, this is a highly readable and thoroughly fascinating introduction to the biology, diversity, and conservation of amphibians and reptiles.

DAVID SEBURN

Seburn Ecological Services, 920 Mussell Road, RR 1, Oxford Mills, Ontario KOG 1S0 Canada

Enjoying Moths

By Roy Leverton. 2001. T & A D Poyser Ltd, London, GB. 276 pp., illus.

This book is a comprehensive introduction to the fascinating world of moths, and general guide to the moths of Britain. Filled with intriguing and useful information, stunning colour photographs, and plenty of illustrations, maps, and drawings, *Enjoying Moths* is a valuable addition to the library of any Lepidoptera enthusiast.

Author Roy Leverton covers an impressive range of information, including, among other things, a general introduction to moth life cycles, colours, and shapes, and details on moth identification, moth lures and traps, moth photography, and moth conservation. His writing is amiable, easy to read, and enjoyable.

What makes this book a delight the author's personal touches. These include anecdotes about, for example, his experiences with cannibalism among moth caterpillars he orders by mail, and his successful efforts to revive an adult moth trapped in a pool of frozen melt water. Leverton also shares private feelings like an instinctive, scalp-prickling sense of danger at approaching a pair of mating Lunar Hornet moths (which look and behave like large wasps) although he knows them to be harmless. And he reveals humorous quirks like his tendency to consume nutritious moth sugar lure

leftovers on nights when he is far from home and has stayed out later than expected.

I learned a lot from this book – the first, and most surprising, discovery being estimates that butterflies make up only 10 to 12% of known Lepidoptera species, with moths filling in the rest! It was also interesting to learn about moth-plant interrelationships, moth lures, and the potential effects of climate change on moth populations.

I especially appreciated the first two chapters – on moth life cycles, colours, patterns and shapes. Yet I must confess that by the time I finished them and came to Chapter 3: Numbers and Distribution, I was becoming dissatisfied with the constant references to species, regions, and habitats unfamiliar to me. I yearned for details relating to my own experience.

It would be helpful if the book's title were a little more specific – something along the lines of *Enjoying the Moths of Britain* – to identify it more accurately.

R. SANDER-REGIER

RR5 Shawville, Quebec J0X 2Y0 Canada

BOTANY

Ainsworth and Bisby's Dictionary of the Fungi

Edited by P. M. Kirk, P. F. Cannon, J. C. David, and J. A. Stalpers. 2001. CAB International, Wallingford. 9th edition. xi + 655 pp., illus.

This is an extremely useful reference book for those studying fungi and lichens. The fact that this is the ninth edition attests to the *Dictionary's* value.

The Preface gives an overview of three major areas emphasized in the new edition; i.e., revision of the classifications of both the Ascomycota and the Basidiomycota; and, third, the integration of the fungi lacking the sexual stage (these are known as the anamorphic fungi, conidial fungi, and/or imperfect fungi) into the overall fungal classification. Thus after each of the nearly 4000 genus names for anamorphic fungi there is a phrase giving its placement; e.g., for the anamorph genus name *Botrytis* the entry is "anamorphic *Botryotinia*." This integration is, unfortunately, not reflected in the Systematic Arrangement of the genera of fungi (an 86 page appendix) where anamorphic names are grouped in an alphabetical list.

A one-page User's Guide helps the user get the maximum benefit from the entries. The paragraph headed Generic names gives the web site where the place of publication of the names can be found. This site is useful but complex and I could not find the database containing the places of publication. Following the User's guide 10 family and nine order names are validly published. There are 41 figures in the book, mostly ink drawings illustrating the differences between, for example, hyphal types, cystidia, predehiscence asci, synnema, hyphidia, and septa. Figures also illustrate life cycles, metabolic pathways, ascus and ascospore development, growth forms, thallus structure in lichens, etc.

The majority of the entries are the taxonomic names, such as genera, families, orders. Most prevalent are the generic names where each entry is composed of the name, the name(s) of the author(s) that described that name, the year the description was published, the major taxonomic group that the name belongs to, the number of species worldwide, and one or a few pertinent references, especially those containing keys to the identification of the species.

Several terms have nearly a page devoted to, in addition to the definition, the history, procedures, current status, and pertinent literature. For example, under the entry "Authors" there are about 200 names of taxonomic mycologists with their birth and death dates, and herbaria where most of their collections can be found. The contribution of these mycologists is, for most, summarized in the text. The heading "Mounting media" includes 11 common fluids used to make slides for examination under the microscope and the formulae for mixing them. Following "Media" there are three pages of evaluation and formulae for the cultivation of fungi in the laboratory. Nearly a page is devoted to the term mycopesticides. Mycorrhiza (that symbiotic association between a fungus and the roots of a green plant), mycetism (poisoning by larger fungi), mushroom cultivation, allergy, air spora, air pollution, predacious fungi, and antibiotics are just a few of the dozens of terms that receive extended treatment. The Lichens have a three-page discussion that includes fungal partners, algal partners, structure, reproduction, establishment, nomenclature, and literature. Unfortunately Brodo, Sharnoff, and Sharnoff's (2001) *Lichens of North America* is not cited, although lichenologists were aware that publication of this significant lichen book was imminent. For other groups of fungi, there were references that I expected to see but did not find, e.g., under Polyporaceae the two volumes titled *European Polypores* (1994) by Ryvarden and Gilbertson are not cited.

This book is a technical reference volume that contains a wealth of information on all aspects of the fungi. One of its strengths are the leads provided to the current literature and more detailed treatments of taxa, methods, phylogeny, etc.

J. GINNS

1970 Sutherland Road, Penticton, British Columbia V2A 8T8 Canada

Illustrated Flora of British Columbia Volumes 1-8

Edited by G. W. Douglas, G. B. Straley, D. Meidinger and J. Pojar (Volumes 1-2); G. W. Douglas, D. Meidinger and J. Pojar (Volumes 3-8). 1998-2002. Ministry of Environment, Lands and Parks and Ministry of Forests (Volumes 1-6), Ministry of Sustainable Resource Management and Ministry of Forests (Volumes 7-8.), Victoria, British Columbia.

Volume 1, Gymnosperms and Dicotyledons (Aceraceae through Asteraceae). 1998. 436 pages.

Volume 2, Dicotyledons (Balsaminaceae through Cuscutaceae) 1998. 401 pages.

Volume 3, Dicotyledons (Diapensiaceae through Onagraceae). 1999. 423 pages.

Volume 4, Dicotyledons (Orobanchaceae through Rubiaceae). 1999. 427 pages.

Volume 5, Dicotyledons (Salicaceae through Zygophyllaceae) and Pteridophytes. 2000. 389 pages.

Volume 6, Monocotyledons (Acoraceae through Najadaceae). 2001. 361 pages.

Volume 7, Monocotyledons (Orchidaceae through Zosteraceae). 2001. 379 pages.

Volume 8, General Summary, Maps and Keys. 2002. 457 pages.

The eight volumes are all in soft cover and measure about 28 × 21.5 cm and a total of 20.5 cm. They are the result of a tremendous amount of work on the flora of the Canadian province which has the largest number of plant taxa in its terrain. This Flora of British Columbia treats 139 families which contain 752 genera with 2717 species plus subspecies and varieties, of which 677 are introduced.

The first seven volumes all have the same introductory information: a foreword regarding the biological diversity of Canada's most western province, the initiation of the co-operative research program in 1992 and 1995, a title page, Canadian Cataloguing in Publication Data, Contributors, Acknowledgments, Table of Contents, Introduction, Format, a figure of Geographical Regions of British Columbia, Database and Taxonomic Concepts.

The order of the family groups, Gymnosperms, Dicotyledons, Pteridophytes and Monocotyledons in these seven volumes can be found in the title information above. Within each group, the families are in alphabetical order with a key to the genera which are then treated in alphabetical order and the species in each genus are keyed and treated in alphabetical order. The description of each species begins with the scientific name in bold face italics followed by synonyms, if any, in regular italics. The next line provides the common name or names in bold face regular print. Below this are HABITAT/Range with inset information and DESCRIPTION with separate lines inset for information under the following headings: General, Leaves, Flowers and Fruits.

The bulk of the first seven volumes is devoted to the generic keys and the most useful descriptive information of usually three species on the left hand pages and excellent line drawings of those species opposite on the right hand pages. This is followed by a list of references, Appendix 1 – Excluded Species, Appendix 2 – Name Changes, Glossary and an Index. Unfortunately, the authors were not provided proofs for the first two volumes before these were printed.

Volume 8 has Acknowledgments, a Table of Contents, a short introduction, a table listing the Composition of the Flora by families, genera, species, subspecies, varieties, native taxa, and introduced taxa of the whole flora, Phytogeography which includes information on Cosmopolitan Species, Bipolar Disjuncts, Circumpolar Species, Amphiberingian Species, North American Maritime Species, North American Radiants, Cordilleran Species, Alaska-Yukon-Northwestern British Columbia Endemics, Pacific Coast Endemics and British Columbia Endemics. This is followed by a useful Key to Families of Vascular Plants in British Columbia, a Key to Aquatic/Semi-aquatic plants in British Columbia and related references.

This is then followed by an Addenda/Errata chapter of 52 pages which provides information on minor corrections in the first seven volumes, 16 new taxa now known from the province and 13 new illustrations for taxa previously recorded for the province.

Distribution maps are provided in the eighth volume for 2871 vascular plant species. Dots and circles depicting known populations are approximately 70 km in diameter and may mask many sites in the same area. In the case of trees, shaded polygons are provided in lieu of dots. The circles appearing on some of the rare vascular plant maps indicate that the collection at the site was taken prior to 1950. An index to the families, genera, species, subspecies and varieties treated in the eight volumes completes the work.

The authors are to be congratulated for their efforts in completing this enormous work.

WILLIAM J. CODY

National Program on Environmental Health, Agriculture and Agri-Food Canada, Research Branch, Wm. Saunders Building, Central Experimental Farm, Ottawa, Ontario K1A 0C6 Canada

Ontario Wild Flowers

By Linda Kershaw. 2002. Lone Pine Publishing, 10145-81st Ave., Edmonton, AB V6E 1W9. 144 pp., illus. $19.95.

This book will be a most valuable introduction to Ontario wildflowers not only to young people, who are just beginning to admire the plant colours as the flowers develop through the spring and summer, but also for all ages beyond.

The first five pages present a colour guide to the flowers of the 101 species presented in this book. This is followed by "Why Learn More About Wild Flowers?", "What is a Wildflower?", "Tips for Identifying Wildflowers", "To Pick or Not to Pick", "Danger, Beware!", "Organization of the Guide", "Information for Each Species", "Fun with Flowers", and "Using a Key to Identify Wildflowers". All these present useful and most informative information. The "Key to the Wildflowers in This Book" has a key layout I have never seen before. Fine line drawings of the flower parts of all the wildflowers treated in this book are a part of the key and are accompanied by the common name and the page number on which each of the 101 may be found. On each of these pages there are two beautiful pictures, the larger one which displays the plant and the smaller one which displays the close-up of the flower or flowers. Beside these flower pictures is a most interesting paragraph on the history, reproduction, uses, and association with insects, animals, and people. This is followed by a short description of the plant, its leaves, flowers, fruits, time of flowering, habitat, distribution, and suggestions about picking or not picking.

This most interesting and colourful part is followed by a glossary which describes the various parts of the plants accompanied by fine line drawings of the various parts, suggested reading of other publications, a wildflower checklist, and common and scientific family names with page numbers where they may be found and an index of common and scientific names. An excellent photo of Linda Kershaw and her family completes the work. Congratulations!

WILLIAM J. CODY

National Program on Environmental Health, Agriculture and Agri-Food Canada, Research Branch, Wm. Saunders Building, Central Experimental Farm, Ottawa, Ontario, K1A 0C6, Canada

ENVIRONMENT

Remote Sensing for Sustainable Forest Management

By S. E. Franklin. 2001. Lewis Publishers, Boca Raton, 407 pp. U.S. $99.95.

This book sets new standards on forestry and remote sensing. It is a must for foresters as well as for remote sensing scholars and people interested in the management of landscapes. It is not only "about understanding pixels", it is about the world we live in and its sustainable management. It shows how peaceful satellite imagery can be used to manage one of the most precious resources for the benefit of mankind: the global forests. Remote sensing applications are often applied as a technological fix. Instead, and as emphasized in the text of this book, remote sensing and other data are still not sufficiently used by forest managers to make best-informed and wise decisions. How easy does one have to make it for the managers so that good and long-term decisions are made towards a healthy planet? Indeed, the text shows that translating remote sensing data into valuable information is not always a simple task. Forestry as well as remote sensing are multidisciplinary research fields; a concept that most agencies and their bureaucrats worldwide still have difficulties coping with. It is easy to comprehend that only a valid research design converts remote sensing data into relevant information.

Based on his successful career in the field of remote sensing, author Franklin knows his material intimately. The reader will appreciate the inclusion of the history of remote sensing. The breakthrough of remote sensing came in 1968 but challenges still remained; e.g., with aerial photography still competing with remote sensing imagery for some applications, even trying to put specific remote sensing applications into doubt. In many cases, geo-referenced pixels (from remote sensing or orthophotos) are statistically more powerful than polygons (from interpreted aerial photography). Obviously, the field of remote sensing has still not even reached its level of maturity; thus, it will become the technique of the future. However, in the field of remote sensing there is still the conflict between the producer and the user. "It can be done with Remote Sensing" but "is this of use to you"? This book definitely helps to solve that issue.

As shown in the book, remote sensing has one of its strengths in forest management applications dealing for instance with forest cover types, determination of forest conditions, landscape change detection, fire and forest defoliation. In addition, the book shows nicely how remote sensing has itself established as the method of choice for forest inventory, and estimations of biomass and even forest structure. Ecological research topics like the role of scale and of modelling are also

discussed. It is nice to learn also about remote sensing applications in situations where modern forest harvesting practices such as partial harvests are used. In addition, hot topics like remote sensing and landscape metrics, as used in the new field of landscape ecology, are delivered in a very readable and informative fashion. The classification of remote sensing images makes up another major component in this book.

In order to achieve its goals and expectations, remote sensing requires a technological and organizational infrastructure. As Franklin emphasizes, the advantages of remote sensing applications are its costs, its accuracy, and the effort, for instance when compared with a large-scale aerial photo approach-based inventory.

The book includes also excellent reviews on the currently available 19 sensors such as LIDAR, IKONOS, IRS, AVHRR, Landsat TM, MSS, RADARSAT, CASI airborne and many others. Forthcoming sensors of the future are explained as well. Certainly, in order to be useful, remote sensing needs to be freely available and easy to use in order to warrant that the best possible management decisions are done. This subject was devoted an entire chapter of its own: The acquisition of imagery. A very relevant discussion on criteria and indicators of sustainable forest management is presented over many pages. Fitting into the context, important issues like biological diversity, conservation of soil and water and global ecological cycles are included, too. The text is lively but words are carefully chosen; the formerly Calgary/Alberta-based author uses many local examples, but also applies data from his work in Canada and elsewhere; he cites his colleagues worldwide in a representative fashion.

Based on my own work experience, I found the following citation in the book "... casual attitude towards geographical information and mapping sometimes found in forestry ..." to be very true for many professional fields, such as biology. It is also true that "...GIS is no simple process". As Franklin points out nicely, every remote sensing product will eventually be used in a GIS application, and thus, one still wonders why the remote sensing and GIS fields have not merged, yet, or develop products in shared formats?

This book brings all these points across by using an error-free, structured, well written, and clear text. Some readers might find the book extensive, but the information delivered is superb and unique for its kind. The strength of this book is that it summarizes for the first time the complex remote sensing and forestry and management topic. For my taste, the chapter on sustainable forest management could perhaps place stronger emphasize on the key concept that "not more wood may actually be cut than what is really re-growing". Accurate inventories are needed. Using the soft term "sustainable forest management" could be somewhat misleading, and could be interpreted as a play with words; perhaps "sustainable forestry" is the clearer definition. However, these things are well compensated and clarified when the author talks about "Forestry in Crisis". "There is ample evidence for a global failure by society to practice sustainable management...", or "By some accounts, almost half of the original Earth's surface is gone, much of it removed within last 30 years". No doubt, remote sensing has contributed to these statements and to global landscape conservation. Nevertheless, political will and public education are also required to implement these findings, produced by complex machines located in the orbit, into the "global society" in a democratic way. Perhaps in a future update of this book it could also be elaborated on how the "undeveloped" world has benefited from remote sensing applications, and who funded these.

The text is based on 60 pages of scientific references, all correctly cited and without apparent typos. The very well-organized index makes this book an outstanding reference for forest managers, students and environmental landscape scientists alike. For the sake of a healthy planet, one really wishes that many forest managers and decision-makers will actually read, understand, and apply this book. After the publication of this book they have no excuse anymore.

FALK HUETTMANN

Geography Department, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2N 1N4 Canada

Present address: Biology and Wildlife Department, Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775-700 USA

Snow Ecology: An Interdisciplinary Examination of Snow-Covered Ecosystems

Edited by H. G. Jones, J. W. Pomeroy, D. A. Walker, and R. W. Hoham. 2001. Cambridge University Press, New York. xx + 378 pp., illus. U.S. $80.

As its title suggests, *Snow Ecology* examines snow and its effects from many points of view. The book is divided into seven multi-authored chapters or review papers. The chapter titles provide a good summary of the entire book: Snow Cover and the Climate System, Physical Properties of Snow, The Chemistry of Snow: Processes and Nutrient Cycling, Microbial Ecology of Snow and Freshwater Ice with Emphasis on Snow Algae, The Effect of Snow Cover on Small Animals, Snow-Vegetation Interactions in Tundra Environments, Tree-ring Dating of Past Snow Regimes.

Given the wide range of topics covered the book is best viewed as a reference book or textbook rather than something to sit down to read from cover to cover. To this end the book includes a very comprehensive table of contents (5 pages). This allows the reader to easily locate a topic within a chapter. In addition, there is a 20-page glossary of terms and a fairly thorough index. I was also impressed that most chapters concluded with suggestions for future research needs, although not all chapters explicitly listed this as topic in the table of contents. The book is profusely illustrated with black-and-white drawings and graphs. There are four pages (two sheets of glossy paper) with colour illustrations that added little to the quality of the book but one wonders what effect they had on the cost.

It should be stressed that this book's emphasis is on snow, not winter. Hence there is only one slender chapter on animals and this is focused on winter active invertebrates and small mammals. Topics such as hibernation, or adaptations in birds or large mammals to winter conditions are beyond the scope of the book. This is not a criticism, as the editors have carefully avoided the broader term winter ecology, but it still might mislead some readers.

Overall, the writing is clear and strong. There is no poetic language here. The statements are fully referenced. While this is not the definitive book on winter ecology it clearly is an excellent guide to snow and how it affects the landscape.

DAVID SEBURN

Seburn Ecological Services, 920 Mussell Road, RR 1, Oxford Mills, Ontario KOG 1S0 Canada

Seabirds and Atlantic Canada's Ship-Source Oil Pollution

By F. Wiese. 2002. World Wildlife Fund, Toronto, Canada. 82 pp., illus.

The public seems to have a love-hate relationship with oil. Oil allows for high salaries and contributes to civilisation, but it also can create severe pollution. As this report shows well, chronic offshore oil ranks among the most severe pollution problems in the world.

"Many people consider Canada to be one of the leading nations in environmental conservation in the world". However, the still conservative estimate of 300,000 dead Canadian seabirds due to chronic oil pollution and presented in this report is shocking, to say the least. Besides a seabird population issue this is also a major animal care issue: over 300 000 animal individuals are suffering and are dying a gruesome death. As this informative report emphasizes, for each oiled seabird found in Newfoundland one can assume that at least 10 more have died.

Together with several individuals devoted to the issue of marine oil pollution, author Dr. F. Wiese studied seabirds and their oil-related mortality for many years. His report on chronic offshore oil pollution is structured in two parts: The Problem (11 chapters) and The Solution (8 chapters); four appendices, a list of abbreviations, and some references are also given. Half of the report deals with OSIRs (Oil Spill Intelligence Reports 1997-2000), presented in Appendix 4. OSIRs are only accessible for a few signed-up members, and it is great that Wiese's report provides the wider public with an opportunity to access this information. Besides reporting baseline numbers of seabird mortalities and oil pollution incidents, other highlights of this document are presented to a wide audience dealing with ocean modelling, detectabilities of oiled birds on a beach, drift block experiments and emphasizing how important such methods are to address the chronic offshore oil pollution efficiently and in accurate terms.

"Most of those in the marine industry carry out their operations in a safe and environmentally responsible manner." This statement is somewhat in contrast to the fact that oiled birds keep washing up on shorelines worldwide which suggests that national legislation and international conventions and guidelines are not being followed or that they are inefficient. "The illegal discharge of oil from ships into the world's oceans is a global problem that affects the entire marine ecosystem". This calls for a well-designed global oiled bird survey; e.g., citizen- and volunteer-based marine and beach surveys.

From this nice report it becomes quickly obvious that the history and track-record of chronic oil pollution, a

by-product of the current civilisation, is not an environmental success story. Instead, the current progress for trying to keep the (marine) environment clean presents more of an international embarrassment. It is still difficult to understand why the "burden of proof" for chronic oil pollution is not on the industry side. After reading this report and its seabird facts one cannot deny that oil pollution equals environmental massmurder.

It is correct that the Canadian legislation extends the enforcement of shipping, environmental, and wildlife law to the 200-mile exclusive economic zone. However, some federal legal decisions have restricted these laws to the 12-nautical-mile territorial zone. Offshore pollution monitoring flights are made by Transport Canada and by the Canadian Coastguard; the Department of National Defence and Department of Fisheries and Oceans are encouraged as well. Although the Canadian Shipping Act, the Migratory Bird Convention Act, the Canadian Environmental Protection Act, and the Fisheries Act deal with oil pollution issues, suspected ships have rarely been turned back to a Canadian port for further investigations. Only the Migratory Bird Convention Act protects migratory seabirds from oil-related offences; but so far, only five vessels have been charged. Knowing that approximately 2500 offshore oil spills are reported per year in Atlantic Canada, one gets quickly an idea of the issue. Obviously, pollution pays ... and as the report convincingly shows, the pollutor gets almost rewarded due to the competitive business advantage when not punished. Atlantic Canada is simply the cheapest place to dump bilge oil on the Great Circle route between North America and Europe. No doubt, the enforcement needs to be stronger in Canada, higher fines are required, and on board disposal facilities, increased monitoring, increased awareness, and other measures are necessary. Even the European Union uses RADARDSAT (SAR), a satellite image product from Canada, in order to trace and to monitor offshore oil pollution.

As Wiese's WWF report presents, Canada does not really have a national standard for an EDA (Environmental Damage Assessment). It is surprising that the exact number on "how many seabirds are really oiled" is hard to get and not available with high accuracy; accurate numbers seem not to play a role in the legal decision and discussion even! Perhaps court fines should consider a price per oiled seabird, and thus could change the current dilemma?!

This document reports that approximately 40 million pelagic seabirds reside during the year on the Grand Banks off Newfoundland. However, some of the presented numbers are puzzling and might cause confusion for the informed naturalist. It was reported earlier that over 200 000 thick-billed Murres are killed annually during the Murre hunt off Newfoundland. But even now, with chronic oil pollution added, breeding Thick-billed Murres in the Canadian Arctic (the seabird species believed to be affected the most by chronic oil pollution) do not show a significantly declining population trend. Are Canadian seabirds really sensitive indicators of the marine environment? Or are birds from other areas present in Canadian waters, such as Greenland's Thick-billed Murres and Manx Shearwaters from England (both populations are known to be declining), better indicators? More research is required. Some other confusion might arise from the presented population numbers of wintering Eastern Harlequin Ducks, and that no direct relationship is known to exist between the amount of oil spilled and the numbers of seabirds killed. For my taste, some key references such as J. Burger's 1997 book *Oil Spills* would have been a great addition. Of interest might also be the other Canadian seabird oil pollution work in British Columbia by A. Burger, the Festucca Oil Spill Trust Fund, and the Provincial Government. Globally speaking, it might be interesting for the reader to learn how Norway, a country with major offshore oil resources with a very long coastline and huge seabird resources, deals with chronic oil pollution! Perhaps it would also be informative to have a list of all known oil vessel accidents in Canadian waters.

This informative report provides many important details and baseline information on the sligthly overlooked but very relevant chronic oil pollution topic in the offshore waters of Eastern Canada. It focuses on seabirds; but many other species and the entire ecosystem suffer from oil pollution, too. "Chronic oil pollution is an international problem whose solution requires national and international effort".

FALK HUETTMANN

Department of Geography–Earth Science, 2500 University Drive N.W., Calgary University, Calgary, Alberta T2N 1N4 Canada

Present address: Biology and Wildlife Department, Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775-700 USA

Monteverde: Ecology and Conservation of a Tropical Cloud Forest

Edited by N. M. Nadkarni and N. T. Wheelwright. 2000. Oxford University Press, Don Mills, Ontario, Canada. 573 pp., illus. CAN $43.95. ISBN 0-19-513310-2.

This is a gigantic and very important book. Much of our knowledge on tropical ecology comes from only a handful of research sites. Monteverde in Costa Rica is among them. Monteverde has the most spectacular cloud forest anywhere in the tropics; six principal life zones of Monteverde are known: Pacific Slope (premontane moist and wet), Continental Divide (lower montane wet and moist) and Caribbean Slope (premontane rain, tropical wet). As this milestone publication shows, it was the Golden Toad, a spectacular endemic frog species, which made Monteverde really known to the scientific world; it became the symbol of the global amphibian decline. Since 1975, 167 species new to science have been found in Monteverde. For the first time in any neotropical plant species, flower visitation by rodents was documented in Monteverde. Besides many other things, the first Costa Rican nest of a Sunbittern was also described at Monteverde.

Overall, Monteverde represents the best known high-elevation site in Central America. For a long time Monteverde has been known to produce superb research; e.g., 16 PhDs on birds alone. This situation is well reflected in the 124 book contributors from seven countries. More than 140 biologists, artists, photographers and Monteverde residents made this landmark publication possible.

This brilliant book consists of 12 main chapters and of an incredible number of short and fascinating chapters from students and others on selected topics. A great resource is the ten appendixes and the references. Appendix 1 shows a plant inventory list for Monteverde. Appendices 2-10 deal with Orchids, Bromelids, Amphibians and Reptiles, Birds, Mammals and others. The naturalist will appreciate that Spanish and English names are given for vascular plants and for mammals (not for birds).

This great Monteverde book is basically impossible to review: there is so much detail; naturalists, researchers and conservationists will be delighted. Monteverde is known to harbour over 500 orchid species. The chapters dealing with bryophytes, fungi and epiphytes are superb; e.g., reporting on such fascinating topics as epiphytic histosol soils on tree branches, crown humus and pollination. Very detailed climate and hydrology information is provided for Monteverde, too. The entire known Monteverde fauna gets described, including bats, singing-mice and "vicious" beasts such as the ant-decapitating fly (*apocephalus*). As the book explains nicely, birds are the "poster children" of conservation efforts. Thus, a superb detailed bird chapter covers many relevant research fields in current ornithology (the expertise of co-editor N. Wheelwright). As a reflection of the expertise of the other editor (N. Nadkarni) a major and significant contribution of this book deals with vegetation, fern, trees and canopies. Also, nitrogen input is mentioned, a topic which is often even lacking in advanced studies of northern hemispheres. In addition, volcanic and tectonic events as well as palaeoecology are covered. Such a descriptive detail does true justice to the tropical ecosystem and its biodiversity.

Particularly the Conservation Chapter is great lecture material and a superb overview about the field, and about (philosophical) reasons for conservation.

This book has also a nice and detailed documentation about local livestock and crops, which are so often ignored in many other tropical studies and publications. Even pre-historic cultures and settlements are well described as is the historical use of large mammals by locals such as the dairy history and the agro-ecology of coffee. Very informative are the chapters on pro's and con's of Ecotourism. Until 1977 tourists were relatively uncommon, now 50 000 eco-tourists visit Monteverde annually.

Certainly, many fascinating research questions are addressed in this book, such as sex ratios of trees, radio-tracking studies of birds and the "pointer hypothesis" for hummingbirds. An interesting link is presented for Quetzals, tree bark, and a medication against AIDS. Besides many others, research questions deal with the many bizarre behaviors exhibited by birds; e.g., communal social behaviors of Brown Jays, the chorus of Three-wattled Bellbirds and dual-male duets of Long-tailed Manakins. The obvious strengths of the Monteverde bird research are autecological studies and investigations of bird-plant interactions. Current research short-comings and future research topics are addressed, too. For instance, the lack of soil studies is emphasized for Monteverde. Cloud forests have not been well collected and high quality reptile population surveys are needed.

In the light of the delicate land owner balances, approaches to "Conservation Easements" in Monteverde are also presented in this book. The Monteverde Cloud Forest was among Costa Rica's first "Debt-For-Nature Swap". It was relatively easy to preserve Monteverde because, at the time action was initiated, it was nearly inaccessible. In 1951, a band of fewer than 50 North American Quakers bought land and settled in Monteverde. Their pioneering conservation efforts are well described here. Major themes at Monteverde include deforestation due to cattle grazing and agriculture, wood harvesting and exploitation of non-wood forest products and the effect of the Arenal Hydroelectric Project. The region has received international conservation support from agencies such as CIDA and WWF-Canada. Charismatic wildlife symbols such as the Quetzal were used to protect the forest and its fauna. In Monteverde the Scarlet Macaw is already locally extinct, and the White-lipped Pecary has not been seen

in the recent decades; it was last known to be present in the 1930s and 1940s. The Giant Anteater was also extirpated within decades after settlement, and Tapirs are now considered endangered. As a result of deforestation, range extensions of birds occur, such as the increasing number of Brown-Jays. Also, the book reports on "escaped" plant species from Africa, and on recent immigrants to Monteverde such as Africanized Honey Bees.

As the book discusses in great detail, population fluctuations in the area may be the norm rather than the exception. The affect of El Nino might be reflected by Monteverde's fauna, for example in the crash of Harlequin Frog populations. The "standard of proof" is an issue of debate in population studies. Are there sufficient long-term data for Monteverde to judge how unusual the amphibian declines really are in the context of natural demographic variability? The drastic crashes of Golden Toad, Harlequin Frog and Fleischmann's Glass Frog in 1987 are definitely part of a global pattern. Underlying reasons are discussed in this book.

On top of the existing population crashes, additional features make conservation topics even worse such as uncontrolled market-hunting: a singing male of a Black-faced Solitaire is worth 100 US$ in San Jose, and it is known that Orchid collection presents an international threat.

One cannot escape the inherent ideology of this book and of Monteverde; e.g., the "no take" attitude and strong conservation beliefs. Monteverde is part of the "Children's International Rainforest" campaign and strongly underlies the influence of many international conservation organisations. In this context, it is fascinating to learn from this book about the various competing NGOs (non-governmental organizations) and even about the lack of a centralized library, a digital reference pool and other relevant databases for Monteverde.

The editors claim that long-term studies and monitoring are carried out at Monteverde. However, I find when it comes to consistent and high quality long-term data, and to quantitative abundances, this book is less strong. The book does not mention centralized databases available for free over the WWW, such as implemented so successfully in CONABIO, Mexico. As a minor drawback, most of the presented maps are really hard to read, which might be a direct reflection of the lack of spatial ecology approaches in this book. All figures and photos are in black-and-white (which I find suits the style of the book perfectly).

In summary, despite deficiencies, this is an outstanding and highly recommended book; a great and long-term achievement of the many people involved with Monteverde. Indeed it belongs on the book shelf side-by-side with major publications about tropical ecology such as La Selva/Costa Rica, Barro Colorado Island/ Panama and Coch Cashu/ Peru.

FALK HUETTMANN

Geography Department – Earth Science, 2500 University Drive N.W., University of Calgary, Calgary Alberta, T2N 1N4 Canada

Present address: Biology and Wildlife Department, Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775-700 USA

Plundering Paradise

By Michael D'Orso. 2002. Harper Collins Press, U.S. $24.95. xix + 345 pp., illus.

This is a book about the Galapagos; not the usual wildlife account, but the human side of island life. My initial reaction to the opening pages of this book was negative. The author's attitude seemed to be cynical and he appeared to have missed the key concept of the Galapagos Islands. Rapidly though, I realized that this man was one of the best writers I had come across in a fair while, even if he is unnecessarily a little crude on occasion. I sensed he despised the Pollyanna attitude of ecotourists while describing the contribution they made. However, I really questioned if he could see the marvel that is Isla Galapagos.

Unlike most authors (who write about the amazing Galapagos wildlife) this one writes of the lives of the people who live and work on the Galapagos Islands. He includes unfaithful spouses, corrupt officials, the power and money hungry, the uncaring, as well as people trying to do the best to preserve the natural heritage. While he focuses on the islanders, it is impossible for him to neglect the political and administrative influence of mainland Ecuadorians. The key concern is that the mainlanders will favour exploitation of nature over protection. Not surprisingly, there is more focus on the evils that beset the Galapagos than on the positive progress. But that is human nature and we all love a scandal.

I did wonder why he travelled to these remote islands to get material for a book. Each country has bad politicians, corrupt officials, vested interests, questionable use of tax money, and cheating spouses. In particular, in D'Orso's country (the United States) there is a real concern that under the current administration, environmental issues are being overridden by industrial interests. However the author reveals that the problems are far more acute in Ecuador than in North America. I have seen recent estimates that at least $2 billion is plundered from Government funds each year by Ecuadorian political leaders. One recent President, Abdala Bucaram, is said to have spent his time in karaoke bars

and fled the country with millions of stolen dollars. Many of Ecuador's 12 million people, of whom 70% are considered poor, blame the state of their economy on this pillage.

So what kind of people does D'Orso find in these remote islands? First there are the "native" inhabitants – where native means those who were born on the islands. This could mean people with a wide variety of ancestral origins. The first true settlers were Norwegian, but most today are from Guyaquil and Quito. Often these people are the uneducated poor and it is difficult for them to benefit from the ecotourist trade (they do not speak English, etc.)

Then there are the "adventurers", people who came looking for something inexplicable and found it in these islands. They are shopkeepers, hoteliers, missionaries, and other western occupations. Photographs of many of these people precede each chapter. To these are added policemen, park employees, and, of course, politicians.

Another group is the research people, mainly associated with the Darwin Research Centre. These are outsiders who come for limited periods, although some do stay for many years. The other outsiders are the tourists. Mostly they are ecotourists who come to marvel at unspoiled nature. If D'Orso is to be believed, some women travellers expect more from their male guides and some of these young men are happy to oblige! One important characteristic of both these groups is that they do not rely on the Galapagos to earn their living.

Finally there are the plunderers. These are mostly commercial fishermen, poor people from the mainland in ships supplied by the rich and influential, who reap illegal harvests of sea-cucumbers (a big seller in Asia as an aphrodisiac), sharks – or at least their fins, and other sea creatures. Joining them are people who slip in to protected areas to hunt or fish for fun.

By going through the lives and stories of these individuals we begin to understand the real history of the human Galapagos. It is not as pretty as the non-human story, but it is most interesting in a gossipy way. The author shows a supercilious attitude towards the islands' charms and the visitors they attract. Yet I often feel "The author (lady) doth protest too much" (apologies to W. Shakespeare) on these issues. Between lines, you can sense that D'Orso is in awe of the natural wonders and realizes the enormous importance of the ecotourists. His descriptions of the birds, reptiles, and scenery are very accurate and poetic. He clearly respects those people who crusade against the islands' many wildlife problems.

Visitors, both past and future, will get a lot out of this book. Not that all of us are insensitive to Ecuador's woes, but the author delves more deeply at a personal level than we would ourselves. Not only will the reader get a sense of daily life, but will learn more about the conservationist's struggle. The group that is trying to rid each island of goats, pigs, and rats is a very tough and formidable team. The hunters have a strenuous, arduous and uncomfortable job. They must also fight for money (it costs millions for weapons, helicopters, and supplies) and stave off the well-meaning but impractical animal rights supporters. Some of this material is very intriguing.

Recently Lucio Gutiérrez won the presidential election after promising to fight corruption. He gained much support with promises to help poor indigenous people. If he is to succeed he will need to keep his support from the social movements, the Indians, and get support from the business sector and the international financial community. He has to do this when his supporters do not have real power, which still lies with a privileged minority of people of Spanish origin. This will be a formidable task, but if he is successful it will bring improvements to the lives of those on these enchanted isles that D'Orso chronicles in this book. So there is hope, we hope.

ROY JOHN

2193 Emard Crescent, Ottawa, Ontario K1J 6K5 Canada

Birds of the Untamed West: The History of Birdlife in Nebraska, 1750 to 1875

By James E. Ducey. 2000 [but released for review in 2002]. Making History, Omaha, Nebraska. 300 pp., illus. U.S. $25.00.

This book is a valiant attempt to report the ornithological history of Nebraska to 1875. Commendable strengths include Chapter 1, which discusses the bird knowledge and lore of the native Americans, the Lakota, Missouria, Otoe, Omaha, Pawnee, Ponca, and Winnebago tribes. Native language bird names are provided when available. Chapter 2 provides a summary of historic explorations, most of which were made by men merely passing through the state while heading farther north and west. Many of these explorers came through in autumn, after the bird breeding season was over. Exceptions were Lewis and Clark, in Nebraska from 11 July to 8 September 1804, and Thomas Say with the Major Long expedition, present from 19 September 1819 to 6 June 1820. Chapter 3 provides a succinct account of the early bird habitats, and Chapter 4 tells which species were found in each of these habitats. Ducey provides, in square brackets, occasional corrections of obviously misleading statements in Aughey's 1877 paper. The list of references

I found impressive. Thirty-three early illustrations add to the interest and attractiveness of the book.

For each observation, the name of the current Nebraska county is provided in upper case letters: "shouting" in modern computer parlance and to me a bit annoying. Unlike Robert E. Stewart's North Dakota book, Ducey does not provide a map showing the location of each county, forcing the reader to provide himself with a Nebraska state map before reading very far.

Before listing the shortcomings of Chapter 5, the last half of the book, I chose to use Myron Swenk's historical articles in *Nebraska Bird Review* (in the late 1930s) as a veracity check. I was not too surprised to find that Swenk had, in the late 1930s, provided more detail and better documentation than Ducey. If one takes the Lewis and Clark expedition as an example, Swenk used a not excessive seven pages, including a map showing the progress day by day, consulted original, primary sources, and gave more detail about extant diaries of several members of the expedition. As a further check, I compared the four-plus pages of Nebraska citations in Gollop's Eskimo Curlew monograph with Ducey's account, which again was less complete.

Chapter 5, a List of Species, occupies 110 pages; it lists excavated faunal remains from various forts and Indian camps, and is a useful compilation that leads the reader to original sources. Sadly, Ducey fails to place the verbatim accounts of each species in the explorer's words, indicated by quotation marks or a different font. As a result, one can rarely differentiate fact from Ducey's speculation, extrapolation, and "best guesses." His terminology and presentation are inconsistent, especially concerning whether an individual species is a migrant or a resident, and whether or not there is specific evidence of breeding. His use of "migratory species" is a less satisfactory term than "migrant." Far too often, the term "potential breeder" is used without evidence of dates or localities for eggs or young. Clearly, a conventional publishing house would have provided the outside editorial assistance that this book lacks. The index is incomplete.

In spite of my caveats, especially the idiosyncratic presentation of the species list, anyone interested in the history of ornithology in Nebraska will find much of interest in this inexpensive book.

C. STUART HOUSTON

863 University Drive, Saskatoon, Saskatchewan S7N 0J8 Canada

MISCELLANEOUS

The Emperor of Nature: Charles-Lucien Bonaparte and his World

Patricia Tyson Stroud. University of Pennsylvania Press, Philadelphia. 371 pp., illus. U.S. $34.95.

Patricia Tyson Stroud deserves the highest commendation for this superb biography. She has dug deeply into a virtual treasure trove of European and American archival sources, including unpublished letters in the possession of the Bonaparte family. She has unearthed numerous illustrations of people and places. She details the exceedingly complicated relationships, intrigues, and political machinations within this royal family. The first chapter of this book reads like an opera plot.

Charles-Lucien Bonaparte, the nephew of Emperor Napoleon Bonaparte, enjoyed the wealth and prestige accorded royalty, but, as will be seen, suffered as much inconvenience as benefit. When Charles-Lucien was only seven, his parents chartered an American ship to take them to the United States with their retinue of 46, including 30 servants. They put in to a port in British-held Sardinia in a storm, were taken captive, sent to England and kept under virtual house arrest for four years until Charles-Lucien's uncle, the Emperor Napoleon, was defeated, exiled, and sent to Elba. Since Charles-Lucien's uncle Joseph, the former King of Spain and of Naples, had no sons, he wished to marry two of his daughters to sons of two of his brothers, in the hopes of reviving the Napoleonic succession. Thus Charles-Lucien was married to a first cousin, Zenaide, whom he had not previously met. They spent their honeymoon visiting natural history museums in Frankfurt, Munich, and Milan.

Charles-Lucien arrived in the United States in September 1823 as a brash 20-year-old naturalist, "spirited, dashing, mettlesome and fiery." The young couple settled not far from Philadelphia near Joseph Bonaparte, the bride's father and the groom's uncle. Two of their children were born in the United States (but they had another ten, the last born in 1843). In Philadelphia, Charles-Lucien joined the American Philosophical Society and the Academy of Natural Sciences. Later dubbed by T. S. Palmer as "the father of descriptive ornithology in America," Charles-Lucien Bonaparte "laid the foundations for the study of nomenclature," as Witmer Stone put it. Through intensive study of the descriptions in and those made after publication of Alexander Wilson's nine-volume, 1814-1819 *American Ornithology*, Charles-Lucien published five instalments of "*Observations on the nomenclature of Wilson's Ornithology*," calling attention to the errors and omissions in Wilson. This gained him the enmity of George

Ord, who had edited the final two volumes after Wilson's death in 1813. On the other hand, Charles-Lucien became friends with John James Audubon and Thomas Say. Say appreciated his skills and gave him access to skins of new bird species, including the Burrowing Owl, collected on Say's expedition to the Rocky Mountains in 1819-1820. William Cooper, secretary of the Lyceum of Natural History in New York, the forerunner of the New York Academy of Sciences, became a close friend and published Charles-Lucien's summary of the Genera of North American Birds in the *Annals* of the Lyceum. After Charles-Lucien returned to Europe early in 1828, Cooper edited and saw through the press the third and fourth volumes of Charles-Lucien's major American work, which appropriated Wilson's title, *American Ornithology*, but carried a more accurate subtitle, *Natural History of Birds Inhabiting the United States*.

Once back in Italy, Charles-Lucien masterminded annual scientific congresses from 1839 to 1847 at Pisa, Turin, Florence, Padua, Lucca, Milan, Naples, Genoa, and Venice, even though each was a political powder-keg. The Naples conference was in fact a precursor to the Italian revolution. He turned his attention away from birds and wrote *Iconography of Italian Fauna*, in thirty parts (1832-1841), and a *Manual of Fishes* (1840). He became a deputy in the Roman parliament in 1848 and vice-president of the constituent assembly in 1849, taking much time away from his work in scientific classification.

Because of his involvement with the republican movement, the royalist turncoat Charles-Lucien was forced to flee Italy in July 1849. A "man without a country," exiled from Italy (though Zenaide stayed) and denied permission to stay in France, he sought sanctuary in England. Resolving to commence work on the great project he had contemplated for 20 years, he travelled to Holland. Without access to his notes and books, which were in Rome, he relied on the Rijksmuseum van Natuurlijke Historie in Leiden. There the great collection as well as the hospitality and guidance of Temminck and Schlegel supported and inspired his work, and there began his last great work, *Conspectus Generum Avium*, which was intended to include all known species of birds. During his researches he visited collections in Holland and Germany and corresponded with the leading naturalists throughout the world. Volume 2 of the work was never completed, and the portions produced have an extremely complex and uncertain publishing history, yet the work is (apart from Linnaeus' *Systema Naturae*) the greatest single-author source for new species and genera of birds.

In 1850, the French authorities allowed him to move to Paris and six months later, in February 1851, restored his French citizenship. Charles-Lucien died in Paris, apparently of heart failure, on 29 July 1857.

There is far more detail about political intrigues and machinations in this book than one would encounter in a biography of any other naturalist. Sadly, Stroud is not an ornithologist and hence is not in a position to evaluate, criticize or understand Bonaparte's brilliance as a taxonomist and nomenclaturalist. The inclusion of new taxa first named by Bonaparte would have made a valuable addition (Peters' *Birds of the World* includes 141 bird genera and 181 bird species described by Bonaparte and held by Peters to be valid). A further list of new fish and other organisms named by Bonaparte would add greatly to these numbers. Bonaparte, in demonstrating his erudition in Latin, composed some monstrously difficult names, and was criticized by many then and since for his practice of naming new genera and new species without sufficient grounds. In addition, nineteen avian species and one avian genus were named FOR Bonaparte by others. However, he did name the dove, *Zenaida*, for his pretty wife.

This book will be of interest to all ornithologists with a historical bent, and to anyone interested in royalty in general or the Bonaparte family in particular. It belongs in every university and college library.

C. STUART HOUSTON

863 University Drive, Saskatoon, Saskatchewan S7N 0J8 Canada

ALAN P. PETERSON

P.O. Box 1999, Walla Walla, Washington 99362 USA

John Keast Lord: Materials for a Life

By Donald B. Baker. 2002. Backhuys Publishers, Leiden, The Netherlands. 65 pp. Euro 22.

John Keast Lord, a veterinary surgeon, was one "of many-sided men of action so characteristic of the Victorian age." He was the naturalist on the British North American Boundary Commission from 1858 to 1862*. He arrived at Esquimalt in 12 July 1858, visited Victoria, Nanaimo, and Beaver Cove on Vancouver Island, and then moved east from the mouth of the Fraser River to Sumas Prairie. In 1859 he collected specimens near and east of present Chilliwack. In 1860, he led a risky journey from Stockton, California, overland to Walla Walla and then Kettle Falls on the Columbia River, to deliver needed mules and bullocks. By April 1862, the 49th parallel had been cleared and completed to the Rocky Mountains; Lord sailed from Victoria back to his native England.

Sadly, Lord's obituaries varied "from the inaccurate to the fanciful or wildly untrue," while authors of recent articles about Lord have been guilty of "the facile repetition of statements made by preceding authors without any evident attempt to ascertain the truth."

In addition to 13 pages about the boundary commission, Baker tells us about Lord's travels to Egypt and his final position as manager of the Brighton Aquarium, cut short by illness, and of his untimely death at age 53. Baker lists the six species named for Lord, as well as the British Museum's specimens he collected along the southern Canadian boundary. There are six pages of references, twelve of footnotes, and two of acknowledgments. This is much the best biographical reference available concerning a little-known naturalist of importance to Canada. It will be of interest to natural historians and belongs in each university library.

C. STUART HOUSTON

863 University Drive, Saskatoon, Saskatchewan S7N 0J8 Canada

*Lord, John Keast. 1866. A naturalist in Vancouver Island and British Columbia. 2 volumes. Richard Bentley, London.

When the Wild Comes Leaping Up: Personal Encounters with Nature

Edited by David Suzuki. 2002. Greystone Books, Vancouver. 235 pp. $32.95.

When the Wild Comes Leaping Up – what a great title. Different, attention-grabbing, dynamic. Those who spend time in the wild can identify – they've felt it leap up many times, like the sub-title, *Personal Encounters with Nature* suggests.

And so I opened the book with great anticipation, expecting to be swept away by one gripping story after another. I was also hoping it would be a collection of Canadian writing, but it wasn't. And it wasn't always that gripping either, because the pieces were very different. Some grabbed me from the beginning and held onto me all the way through with their splendid stories and excellent writing. Others, more intellectual or more rambling (sometimes quite long), reached out less assertively, making me work to enter into the story, sometimes getting a hold of me, sometimes not. Still others did nothing at all for me, although I read each piece from start to finish.

But I'm not going to talk about those. I'm going to tell you about the two stories that gripped me most strongly, and let you decide on the rest of the pieces for yourself if you end up reading the book.

The first was Bill McKibbon's "A Desperate Clarity," about a an unforgettable and dangerous experience he had hiking in the woods behind his house in the Adirondacks. As he points out, it was not an encounter with a large carnivore, or a poisonous snake, or even poison ivy. He stepped on a nest of yellow jackets.

It happened while he was climbing a very steep slope. He writes, "all of sudden, there was the most unbelievable pain washing up my stomach toward my neck. It came so fast, as pure a splash of feeling as if someone had tossed a pot of boiling water in my direction. And it hurt so much, a purity of pain I've never experienced before or since. In my memory it expresses itself almost as a flash of white light."

He describes his desperate plunge back down toward home — his rapidly swelling torso, his rising panic — only to be seized by what he calls a "remarkable set of emotions" and awareness which blurred the boundaries between himself and the world around him. He describes his reactions to things he perceives along the way, feeling genuinely a part of it all – a "high" — before his trip to the hospital. When he returns, things did not return to normal.

"It was as if the tears of pain had irrigated my eyes," he writes, "and for weeks afterward the world seemed in sharper focus whenever I stepped outside.... The layers of insulation between me and the real world had been removed, and now the breeze was whistling through. You could say this new state has a dreamlike quality, but it would have been more accurate to say just the opposite—that it felt as if I had woken up from a dream."

He finishes the story with the following lines: "It is a sorry thing to admit that you're so thick it takes seventy-six yellow jacket bites to pierce you.... But the lesson was well worth the price – that desperate clarity was one of the greatest gifts the world ever gave me. When I try to imagine the holy spirit, I hear buzzing."

Bill McKibbon writes superbly. And he writes honestly. In his story the wild leaps up, literally and figuratively, to give him an unforgettable, illuminating experience — an epiphany. I could probably say, and you can probably tell, it was my favourite story.

The other story that really gripped me was also about an epiphany. In fact, that word is in the title, "Catching an Epiphany." The story is by the editor of the book, David Suzuki, and it, like Bill McKibbon's piece, is about, as Suzuki writes, "my moment of enlightenment."

It is a charming, autobiographical story about excitement associated with the outdoors, particularly fishing. "My very first childhood memory," Suzuki writes, "is one of almost unbearable excitement – my father and

I went to a store to buy a tent so that we could go camping." That camping trip led to a passion for fishing, carried through childhood on the west coast and internment in British Columbia's interior during the second world war, to a new postwar life in Ontario, with continuing outdoor experiences in, as he writes, "the pockets of nature that still flourished" in a much more human-dominated landscape.

His epiphany comes when, back in British Columbia with his young family, he takes his son and daughter to a fishing place he heard about: "a logging road near Squamish that would take us to a river that was supposed to contain good-sized rainbows." It wasn't the fish that were unforgettable that day. It was the long, hot hike in from the road, through "a combat zone where the soil had been churned up by the tracks of heavy machines, and all that remained of the immense trees were huge stumps and roots that projected at garish angles among the slash" and the transition to the remaining forest.

"Stepping out of the glare and heat of the clearing and into the dark, cool cathedral of trees was an absolute shock, like stepping from a hot city street into an air-conditioned building. Embraced by the cool shade of the trees, we inhaled the damp, musky odour of vegetation and decaying tree carcasses. We were enfolded in silence. The children immediately stopped bickering and complaining and began to whisper just as if they were in a church.... I was dumbstruck.... In those few minutes that my children and I had entered into the forest temple, I had recognized the terrible hubris of the human economy."

Looking back through the many memorable and formative experiences of his life, Suzuki realizes that "that inspirational encounter", as he calls it, "with an ancient forest on the edge of a clear-cut was my moment of enlightenment." He finishes with the following lines, "the forest that was my epiphany was felled within weeks of my visit there. What remains is my conviction that we must rediscover our biological place and learn to live in balance with the natural world that sustains us."

These stories were, as the lines on the back cover express, "beautifully written and deeply felt ... testimonies to the transformative powers of the natural world." I was hoping all the pieces in the collection would measure up to that description, but they didn't – for me anyway – though some were more powerful than others. It may simply be a question of personal taste.

I would definitely recommend *When the Wild Comes Leaping Up*. Suzuki's excellent introduction and story, along with McKibbon's piece, make the entire book worth reading. And they get you thinking about your own personal encounters with nature – another rewarding experience.

R. SANDER-REGIER

RR5 Shawville, Quebec J0X 2Y0 Canada

Charles Darwin, The Power of Place

By J. Browne. 2002. Alfred A. Knopf, New York, 591 pp., illus. U.S. $37.50.

In 1881, at the science gathering of the British Association, Sir John Lubbock (1834-1913) was able to observe "the book of Nature was like some missal richly illuminated, but written in an unknown tongue" (page 95; *Fifty Years of Science*, 1895, MacMillan and Co., London), referring to the general consensus prior to the publication of *Origin of Species*. "The graceful form of the letters" he continued, "the beauty of the coloring, excited our wonder and admiration; but of the true meaning little was known..." Much of this was cleared up, or at least shown in the proper light not only with Darwin's published work, but by how Darwin meandered in and around the scientific and social community, and with how he directed his science. He, after all, had a vested interest in the long term viability of his theories, his "children" as he sometimes called them. A year after Lubbock's comments, Charles Darwin died.

Janet Browne's much anticipated sequel to the Darwinian saga documents the "father" of natural selection as well as his "children". Her earlier volume, *Charles Darwin, Voyaging* (Princeton University Press, 1996) chronologically ended with the publication of the *On the Origin of Species* in 1859. In many respects, as the result of her craftsmanship in story-building ending at a pivotal point in Darwin's life, the reader was left in a cliff-hanger state (see Tokaryk 1998), even though his remaining years are well known. Her recent submission, *Charles Darwin, The Power of Place* is a seamless continuation of the earlier volume and duplicates its effort and effect on the reader as a well researched story.

It should be noted that much of *The Power of Place* is as much about Victorian/Edwardian science, politics, society, and religion, as it is of Darwin himself. For Darwin's life occupied an ideal time when educational reform provided opportunities for young and old; the birth of the "professional" science as it chipped away at the "amateurish" tower of enlightenment [By definition I refer to these individuals having as much clout, connections, and good breeding as intellect. But let's not forget that Darwin was part of this amateur group as well, holding no professional chair, and producing

his works from the comfort of inheritance, investments, and royalties of his books]. The ability to mass produce literature making it affordable to the emerging middle and lower classes, whether in the form of books or periodicals, launched a new era never before seen. "Much of Darwin's sudden impact" Browne maintains "was the result of having produced a book of wide general interest just as this wave of periodical reading matter burst into nineteenth-century homes" (page 103). Added to this was Darwin's marketing strategy through individuals like Thomas Huxley (1825 – 1895) who led a "publicity campaign for a reformed, fully scientific, rational England where power should be wrestled out" (pages 135-136) of the hands of those more myopic and aged in nature. The evolutionary torch that he carried was the heaviest and brightest he would ever carry.

It would be misleading to believe that any of the themes and moments visited by Browne have not been previously scanned by other authors [and some of these are very good in themselves; Adrian Desmond and James Moore's *Darwin* (1991, Warner Books, New York) is a very fluid, informed piece]. For example, the details of his extended illness, of course, are probed by Browne. Exploring his dilemma as "if it were a natural history problem" (page 239), Darwin also became reliant on his maladies to avoid public situations and personal hardships [the death of long time friend and mentor Charles Lyell (1797 – 1875) for one]. Or, the lesser known indirect pressure by Alfred Russel Wallace (1823 – 1913) on Darwin with respect to the issue of our own species in the arena of natural selection. It is well known that it was Wallace who initiated the rapid publication of *On the Origin of Species*, but here again, *The Descent of Man* was brought forth by several "taunts" of man's place in nature, some of which were provided by Wallace.

In terms of putting Darwin, the person, in a place in time amongst his environment, his culture (almost like a natural history object himself), no other book comes close. And it is impossible to recommend *The Power of Place* without including *Voyaging*. Together, they are comprehensive and enjoyable. The "Darwin Industry", as some have put it (see Lenoir 1987 for commentary), will no doubt benefit from Browne's efforts. After picking apart the details of his life for so many years, much like a scientific experiment, historians have the ability, the need for the construction of a broader image. *The Power of Place* is a powerful image indeed.

References

Lenoir, T., 1987. Essay Review: The Darwinian Industry. Journal of the History of Biology, 20 115-130.

Tokaryk, T. T., 1998. Charles Darwin, Voyaging [review]. The Canadian Field-Naturalist, 112 186-187.

TIM T. TOKARYK

Box 163, Eastend, Saskatchewan S0N 0T0 Canada

The Dinosaur Filmography

By M. F. Berry. 2002. McFarland & Company, Inc., Publishers, Jefferson, 483 pp., illus. U.S. $65.00.

Paleoimagery, The Evolution of Dinosaurs in Art

By A. A. Debus and D. E. Debus. 2002. McFarland & Company, Inc., Publishers, Jefferson, 285 pp., illus. U.S. $49.95.

The culture surrounding palaeontology, specifically, "dinosaurology", has been growing steadily. Much of this can be attributed to the mass market appeal of the genre exemplified by Steven Spielberg's *Jurassic Park*, released in 1993 based on Michael Crichton's novel by the same title (1990, Alfred A. Knopf, New York). Prior to the movie, dinosaurs, no doubt, played a role in our public imagery of the past but not on the same scale initiated with this highly graphic and "scientifically sound" movie. This is a slightly sarcastic comment on my part; though filled with the latest perceptions of dinosaurs as real creatures and the technical procedures required to resurrect them, the movie was also scientifically flawed often for the sake of visual preferences; see R. DeSalle and D. Lindley's *The Science of Jurassic Park and the Lost World*, Basic Books, New York, 1997. Two of the more recent examples of the cultural icon of dinosaurs are Mark Berry's *The Dinosaur Filmography* and Allen and Diane Debus's *Paleoimagery, The Evolution of Dinosaurs in Art*.

The expected audience for *The Dinosaur Filmography* is small. For those interested in virtually any movie that a dinosaur appeared in, this volume is for you. In alphabetical listing, each movie title is followed by factual information including main credits and cast. This is then followed by a brief synopsis of the plot, followed by commentary. As in *My Science Project* for example, released in 1985, "The T. rex sequence is the highlight, or rather the only light, of the movie" (page 287). The final section reviews the required special effects with some insider knowledge, more useful to the movie fan than the dinosaur fan.

The volume contains a plethora of titles, many obscure, ranging from *Gertie, The Dinosaur*, released in 1914 – "so enjoyable was McCay's [the cartoonist] creation that the animation is still enjoyable for modern audiences" (page 114), to less notable titles like *Teenage Caveman* released in 1958 – "Dinosaur movies

with minimal dinosaurs often focused on other attractions like pretty Darah Marshall [the love interest in the movie], to draw an audience" (page 374). Despite those details it is hard to see the interest in this volume except for the collector of dinosaur trinkets or the sci-fi film buff. Information specifically on dinosaurs, their comparative visual history matched to scientific perceptions, or the basis of their development, is minimal. What saves the book from total obscurity is the fact that the fan base for sci-fi/dino movies is ever increasing.

Something with a little more scientific merit is *Paleoimagery*. Here the evolution of dinosaurs as they appeared on the printed page or museum gallery (or in three dimensional model), is hacked at. This book deals strictly with popular imagery, neglecting the artistic skill required for more precise requirements by scientific illustrations. However, even from the beginning of the era of dinosaur art, like Benjamin Waterhouse Hawkin's (1809–1889) late 19th century illustrative renditions for New York Central Park's "Paleozoic Museum" [a museum has its own colourful, but albeit short history], "his methods were state-of-the-art … rel[ying] on information that was scientifically current" (page 47).

The structure of *Paleoimagery*, however, is puzzling and slightly disrupting. The often short chapters, some only three pages long, leap from an individual artist, then a few short pages later, to a taxon specific chapter like *Acanthopolis*, a now defunct name for a mid-Cretaceous ankylosaur from England. This animal is a good example of the faults of restoration based on fragmentary remains. The type specimen, originally described by Thomas Huxley in 1876, is based on a few vertebral fragments. How does one then come up with a fleshed-out, three dimensional model? The book would have been better served by being a little more linear in its approach, either in chronology of the printed matter, the changing genre of the art, or by artists themselves, who, like Charles Knight, had a major impact on other artists as well as shaping the popular views of fossils in several major museum galleries. The shifting between all these approaches, coupled by the brevity of some of the chapters, is rather frustrating.

Despite the fact that *Paleoimagery* lacks colour illustrations (rather surprising for an art-focused book), the premise is rather valuable. One of the main mandates of science is not only to communicate to the scientific community at large, but also to communicate to a broader, more public audience. The images presented in still or moving pictures, is a real gauge as to how science is publicly perceived. And if we laugh at the latex-suited bipedal dinosaurs in *Unknown Island*, or sneer at John Martin's 1838 conception of *Iguanodon*, maybe through books like the two reviewed here, the images they represent can be used, at least in part, as a reflection of how far we've come and a stepping stone upon which to reach for new visions.

TIM TOKARYK

Box 163, Eastend, Saskatchewan S0N 0T0 Canada

Naturalists: A Journal

Women Travelers: a Journal

By B. Hodgson. 2003. Greystone Books (Douglas & McIntyre, Vancouver). Each unpaginated, illus. $19.95.

Both of these books are primarily blank, unnumbered pages left for the traveler to make notes. The books are illustrated with historical museum images and quotations from historical persons in the field. The Naturalists illustrations and quotes come from natural history and the women travelers from historical women.

My wife found the images and quotes quite interesting and plans to use the journal for a diary of future trips. She recommends it as a great gift for the woman traveler "who has everything". I found the book useful as a journal, but was not greatly impressed by the nature illustrations. The same book without illustrations could be bought at the local stationery store for much cheaper. The 13 × 21 cm format is too big for most pockets, but would fit in a backpack. I would have liked page numbers and perhaps a spot for date and location.

WILSON EEDY

News and Comment

The Boreal Dip Net: Newsletter of the Canadian Amphibian and Reptile Conservation Network 7(1) January 2003

Contents: Editor's Note (Kerrie Serben) — The 7th Annual CARCN Meeting Summary: Winnipeg, Manitoba, Sept 27-30, 2002 (David Cunnington) — Extended Abstracts of Keynote Speakers: Infectious Diseases of Amphibians (Danna M. Schock); Amphibian and Reptile Species at Risk in Canada: The Arrival of SARA (David M. Green) — Field Trip: Narcisse Snake Dens 2002 (William B. Preston) — 2002 CARCN/RCCAR Award Winners (Don McAlpine) — Amphibians in Toxicity Testing (Bruce Pauli) — Le code de déontologie du DAPTF pour la recherche sur la terrain A new code of practice for field studies on amphibians from the DAFTF [Decline in Amphibians Task Force] (Martin Ouellet) — Possible Ways to Incorportate the DAPTF Fieldwork Code of Practice into Field Work (Danna M. Schock) [reprinted from a previous issue of the Dip Net] — Status of the Northern Leopard Frog in the Creston Valley Wildlife Management Area — New Publication Announcement: The Eastern Massasauga Rattlesnake Stewardship Guide [available online www.terra-plex.com/sin/stewardship_guide or www.terra-plex.com/sin/index.asp] (Kerrie Serben) — Membership in CARCN/RCCAR.

For information on membership in the Canadian Amphibian and Reptile Conservation Society/Réseau Canadien de Conservation des Amphibiens et des Reptiles ($10 students, $16 non-students] contact Bruce Pauli, Canadian Wildlife Service, National Wildlife Research Centre, Carleton University, Raven Road, Ottawa, Ontario K1A 0H3. Web site: http://www.carcnet.ca/

Froglog: Newsletter of the Declining Amphibian Populations Task Force (56)

Number 56, April 2003. Contents: Amphibian mortality in a National Park in the North of Portugal (Claudia Soares, Antonio Alves de Matos, J. W. Arntzen, Miguel Carretero & Armando Laureiro) — Ecology and Conservation of the Gunus *Neurergus* in the Zagros Mountains, Western Iran (Nasrullah Rastegar-Pouyani) — DAPTF Seed Grants 2003 (Tim Halliday) — Project SAVE [Saving Amphibian Vital Environments - involving science teachers from North Carolina, USA, and Xalapa, Veracruz, Mexico] (David Wojnowski) — Reports on DAFTF Seed Grants (Tim Halliday) — Froglog Shorts.

Number 57, June 2003, Contents: Houston Toad in Bastrop State Park, 1990-2002 (Andy Price) — Amphibian Conservation in the US Pacific Northwest (Deanna H. Olson) — Over half of Mesoamerican Amphibians Threatened with Extinction (Bruce Young, Simon Stuart, Janice Long & Neil Cox) — California-Nevada Working Group Report (David Bradford) — Rocky Mountain Working Group Report (Stephen Corn & Charles R. Peterson) — Amphibian Declines in the United States (Michael J. Lannoo) — Reports on DAPTF Seed Grants (Tim Halliday) — Froglog Shorts.

Froglog is the bi-monthly newsletter of the Declining Amphibian Populations Task Force of The World Conservation Union (IUCN)/Species Survival Commission (SSC) and is supported by The Open University, The World Congress of Herpetology, and Harvard University. The newsletter is Edited by John W. Wilkinson, Department of Biological Sciences, The Open University, Walton Hall, Milton Keynes, MK7 6AA, United Kingdom; e-mail: daptf@open.ac.uk. Funding for *Froglog* is underwritten by the Detroit Zoological Institute, P. O. Box 39, Royal Oak, Michigan 48068-0039, USA. Publication of issues 56 and 57 was also supported by Peace Frogs www.peacefrogs.com and by RANA and the US National Science Foundation grant DEB-0130273.

Point Pelee Natural History News 3(1)

The spring 2003 issue, volume 3, number 1, pages 1-20, contains: Unusual Invaders of Lake Erie (Joseph H. Leach) [European Flounder, *Platichthys flesus*; Chinese Mitten Crab, *Eriochier sinensis*; Grass Carp, *Ctenopharyngodon idella*; Bighead Carp, *Hypophtholmichthys nubilis*; Pacu, *Calossoma* and/or *Piaractus*, unidentified species); Piranha, *Pygocentrus* and/or *Serrasalmus*, unidentified species; Suckermouth Catfish, species of *Hypostomus*, *Panaque*, *Liposareus*, *Pterygoplichthys*] — Noteworthy Bird Records: December 2002 to February 2003 (Alan Wormington) — Point Pelee Butterflies: Annual Summary for 2002 (Alan Worthington) — The status of the Blue Grosbeak at Point Pelee (Alan Wormington) — Point Pelee Dragonflies: Annual Summary for 2002 (Paul R. Desjardins) — Update on Brown Pelicans in Ontario (Alan Worthington) — News and Announcements — Upcoming Events and Outings.

This newsletter for Point Pelee National Park, Ontario, is published by the Friends of Point Pelee and edited by Alan Wormington (e-mail: wormington@juno.com). Editorial Assistants are Gordon D. Harvey and Michelle T. Nicholson. The web site is www.wincom.net/~fopp/Natural_History_News.htm. Subscription rates are Canada: CAN $20 (one year) or $40 (two years); International: US $20 (one year) or $40 (two years). Send payment (and e-mail address, optional) to The Friends of Point Pelee, 1118 Point Pelee Drive, Leamington, Ontario N8H 3V4 Canada. Issues are mailed in March, June, September, and December. Back issues of volumes 1 and 2 are available for $15 per Volume/ $5 per issue.

Marine Turtle Newsletter (100)

April 2003. 60 pages: Marine Turtle Newsletter 100: A Celebration (B. J. Godley and A. C. Broderick — MTN 100: Looking Back, Looking Forward (N. Mrosovsky) — Concerning Those Things Which We Ought to Have Done: Reflections on the Future of Sea Turtle Research (N. B. Frazier) — Why Do We Do This? (J. G. Frazier) — From Ghosts to Key Species: Restoring Sea Turtle Populations to Fulfil their Ecological Roles (K. A. Bjorndal and A. B. Bolton) — Improved Assessments and Management of Shrimp Stocks Could Benefit Sea Turtle Populations, Shrimp Stocks and Shrimp Fisheries (C. Caillouet) — Challenges for Interdisciplinary Sea Turtle Research: Perspectives of a Social Scientist (L. M. Campbell) — Sea Turtle Conservation along the Atlantic Coast of Africa (A. Formia, M. Tiwari, J. Fretey, and A. Billes) — Marine Turtles in Latin America and the Caribbean: A Regional Perspective of Successes, Failures, and Priorities for the Future (M. A. Marcovaldi, J. Thome, and J. G. Frazier) — Marine Turtle Conservation in South and Southeast Asia: Hopeless Cause or Cause for Hope? (K. Shanker and N. J. Pilcher) — NEWS & LEGAL BRIEFS — RECENT PUBLICATIONS.

The Marine Turtle Newsletter is edited by Brendan J. Godley and Annette C. Broderick, Marine Turtle Research Group, School of Biological Sciences, University of Wales, Swansea, SA2 8PP Wales, United Kingdom; e-mail MTN@swan.ac.uk; Fax +44 1792 295447. Subscriptions to the MTN and donations towards the production of MTN and its Spanish edition NTM [Noticiero de Tortugas Marinas] should be made online at <http://www.seaturtle.org/mtn/> or c/o SEA TURTLE.ORG 11400 Classical Lane, Silver Spring, Maryland 20901 USA.

Recovery: An Endangered Species Newsletter (24)

The June 2003 issue contains: RECOVERY HIGHLIGHTS: Protecting coastal plain — Canada-U.S. effort underway for leatherbacks [*Dermochelys coriacea*] — PROFILE: The ecosystem approach: Recovery planning for aquatic species at risk (Shawn Station and Al Dextrace) NEWS BITES: Crested Myna disappears from North America [last two *Acridotheres cristatellus* died in Vancouver, British Columbia, from collisions with vehicles, after being established since the 1890s, and reaching a population of 2500 in the early 1960s] — PEI appoints advisory committee to protect species at risk — Recovering a rare mollusc [Northern Abalone *Haliotis kamtschatkana* in British Columbia] (Christiane Cote and Laurie Convey) — Volunteers H.E.L.P. Bricknell's Thrush [*Catharus bicknelli*] (Becky Whittam) — RENEW [REcovery of Nationally Endangered Wildlife] Update — HSP [Habitat Stewardship Program] Update — IRF [Interdepartmental Recovery Fund] Update — FIELD NOTES: Pale flyers of the night [Southern Okanagan Basin population of Pallid Bat, *Antrozourus pallidus*] (Daniela A. Rambaldini) — Scientists construct next boxes for snakes [Black Ratsnakes, *Elaphe obsoleta obsoleta* in eastern Ontario] (Patrick Weatherhead, University of Illinois [with Gabriel Blouin-Demers, University of Ottawa]) — Why is the flycatcher in decline [Acadian Flycatcher, *Empidonax virescens*, rare in Ontario] (Bonnie Woolfended) — ANNOUNCEMENTS: Site Seeing — New Publications — Awards [Plover recovery work honoured] — COSEWIC Update [Two Atlantic Cod populations designated at risk] — Upcoming Events — FEATURED SPECIES: Reversing the decline: Conserving the Newfoundland Marten [*Martes americana atrata*] (Brian Hearn).

Published by the Canadian Wildlife Service of Environment Canada, Ottawa, Ontario K1A 0H3. Edited and designed by West Hawk Associates.

Recovery online: www.speciesatrisk.gc.ca/species/publications/recovery/june03/index_e.cfm

Vancouver Aquarium Leatherback Poster

The Vancouver Aquarium Marine Science Centre, with assistance from Fisheries and Oceans Canada, has issued a poster featuring a Leatherback (sea turtle) *Dermochelys coriacea* head and forepart of carapace breaking the surface of the ocean and the question "Do you know this turtle?" This is an appeal to report sightings of Pacific Leatherback Turtles by phoning 1-866-I SAW ONE (1-866-472-9663) to increase knowledge of its distribution and frequency in British Columbia waters.

Leatherbacks are the world's largest living turtle. They are totally marine except for southern temperate and tropical beach nesting by females. A fact sheet included with the poster notes that they reach a maximum of 2.4 m (6 ft.) in total length (snout to tail tip) and a maximum of 916 kg (2015 lbs). They can eat their own weight in jellyfish in a day. Moves of up to 12,000 km and dives to 1200 m have been recorded. World populations are thought to have declined from 115,000 individuals in 1980 to 30,000 at present.

More information and references are available on the Vancouver Aquarium website www.vanaqua.org or contact Carla Sbrocchi, Coordinator, Sea Turtle Conservation Group, Vancouver Aquarium, Marine Centre, Vancouver, British Columbia V6B 3X8; telephone 604-659-3400; Fax 604-659-3515, e-mail: sbroccc@vanaqua.org.

Editor's Report for Volume 116 (2002)

Mailing dates for issues in volume 116 were: (1) 30 November 2002; (2) 14 March 2003; (3) 15 April 2003; (4) 16 May 2003.

A summary of membership and subscriber totals 2002 is given in Table 1. The number of articles and notes in volume 116 is summarized in Table 2 by topic; totals for Book Reviews and New Titles are given in Table 3, and the distribution of content by page totals per issue in Table 4. Council contined making 80% of the annual interest from the Manning Fund and other capital available to *The Canadian Field-Naturalist* to offset the publication cost of northern papers where authors' and institutional contributions were insufficient to cover page charges.

St. Joseph Print Group set and printed the journal. Special thanks are due Emile Holst, and to Cecilia Chow and Cameron Fraser and staff for galleys and corrections. Wanda J. Cook proof-read galleys for number 1, and Elizabeth Morton for numbers 2, 3, and 4. Bill Cody as Business Manager handled all reprint requests and bills and oversaw and proofed the compilation of the Index prepared by Leslie Durocher. Wilson Eedy continued as Book-Review Editor.

Manuscripts (excluding book reviews, notices, and reports) submitted to *The Canadian Field-Naturalist* totalled 100 in 2002, down 15 from 2001. The following reviewed papers that had been submitted in 2002: *Associate Editors*: R. Anderson, Canadian Museum of Nature, Ottawa (8); C. D. Bird, Erskine, Alberta (19); R. R. Campbell, St. Albert, Ontario (3); P. M. Catling, Agriculture and Agri-food Canada, Ottawa (10); B. W. Coad, Canadian Museum of Nature, Ottawa (2); A. J. Erskine, Canadian Wildlife Service, Sackville, New Brunswick (24); D. F. McAlpine, New Brunswick Museum, Saint John (8); D. W. Nagorsen, Victoria, British Columbia (12); W. O. Pruitt, Jr., University of Manitoba, Winnipeg (22); *Others*: R. Aiken, Mt. Alison University, Sackville, New Brunswick; E. M. Baggs, Memorial University of Newfoundland, St. John's; J. R. Bider, Ecomuseum, Ste-Anne-

TABLE 2. Number of articles and notes published in *The Canadian Field-Naturalist* Volume 116 (2002) by major field of study.

Subject	Articles	Notes	Total
Mammals*	13	18	31
Birds	12	2	14
Amphibians + reptiles	3	1	4
Fish	6	3	9
Plants	12	1	13
Tributes	1	0	1
Totals	47	25	72

* includes one feature article of history of Bison introductions at Wood Buffalo Park in 116(1).

TABLE 3. Number of reviews and new titles published in Book Review section of *The Canadian Field-Naturalist* Volume 116 by topic.

	Reviews	New Titles
Zoology	52	46
Botany	8	17
Environment	17	37
Miscellaneous	8	12
Young Naturalists	0	19
Totals	85	131

TABLE 1. The 2003 circulation of The Canadian Field-Naturalist (2000 in parenthesis). Membership totals from Annual Report of the Ottawa Field-Naturalists' Club, January 2003; subscription totals compiled by W. J. Cody. Forty percent of membership dues and 100% of subscriptions go to publication of *The Canadian Field-Naturalist*. Members vote on Club affairs; subscribers and institutions do not.

	Canada	USA	Other	Totals
Memberships				
Family & individual	911 (941)	32 (30)	8 (7)	951 (978)
Subscriptions				
Individuals	164 (189)	65 (63)	5 (3)	234 (255)
Institutions	171 (174)	252 (262)	32 (38)	455 (474)
Totals	335 (363)	317 (325)	37 (41)	689 (729)
TOTALS	1246 (1304)	349 (355)	45 (48)	1640 (1707)

Note: 22 countries are included under "Other" (outside Canada and United States): Austria, Belgium, Brazil, Denmark (2), United Kingdom (9: including 1 to Scotland), Finland (2), France (3: including 1 to St. Pierre & Miquelon), Germany (2), Iceland, Ireland, Japan, Mexico, Netherlands (3), New Zealand, Norway (4), Poland, Russia, South Africa, Spain (3), Sweden (2), Switzerland (2), Trinidad and Tobago.

TABLE 4. Number of pages per section published in *The Canadian Field-Naturalist* Volume 116 (2002) by issue.

	(1)	(2)	(3)	(4)	Total
Articles	119	122	138	117	496
Notes	21	21	0	11	53
Feature	19	0	0	0	19
Tributes	0	5	0	0	5
Book Reviews*	17	23	15	29	84
News and Comment	5	2	2	2	11
CFN/OFNC Reports**	0	3	9	3	15
Index	0	0	0	29	29
Advice to Contributors	1	0	0	1	2
Totals	182	176	164	192	714

*Total pages for book review section include both reviews and new titles listings.
**Includes CFN Editor's reports (issue 2), OFNC Annual Business Meeting (3) and OFNC Awards (4).

de-Bellevue, Quebec; G. R. Bortolotti, University of Saskatchewan, Saskatoon; D. Boyd, Corvallis, Montana; I. Brodo, Canadian Museum of Nature, Ottawa; R. J. Brooks, University of Guelph, Ontario; C. Buddle, McGill University, Montreal, Quebec; L. Carbyn, Canadian Wildlife Service, Edmonton, Alberta (3): J. G. Casey, Narragansett, Rhode Island; J. Cayouette, Agriculture and Agri-food Canada, Ottawa; W. J. Cody, Agriculture and Agri-food Canada, Ottawa (14); K. Conlan, Canadian Museum of Nature, Ottawa; M. Costello, Huntsman Marine Science Centre, St. Andrews, New Brunswick; C. Crompton, Boularderte Centre, Nova Scotia; S. J. Darbyshire, Agriculture and Agri-Food Canada, Ottawa (2); M. Gingras, University of Alberta, Edmonton; E. Haber, National Botanical Services, Ottawa (11); S. J. Hannon, University of Alberta, Edmonton; A. Harestad, Simon Fraser University, Burnaby, British Columbia; S. J. Hecnar, Lakehead University, Thunder Bay, Ontario; C. S. Houston, Saskatoon, Saskatchewan (2); B. Husband, University of Guelph, Ontario; L. Imbeau, Université du Québec en Abitibi-Temiscamingue, Rouyn-Noranda; R. James, Sutherland, Ontario; K. Joly, U. S. Geological Survey, Anchorage, Alaska; E. Kenchington, Fisheries and Oceans Canada, Dartmouth, Nova Scotia; T. Kinley, Sylvan Consulting Ltd, Invermere, British Columbia; C. J. Krebs, University of British Columbia, Vancouver; J. Maunder, Newfoundland Museum, St. John's; L. D. Mech, U. S. Geological Survey, St. Paul, Minnesota; J. D. Montgomery, Susquehanna SES Environmental Laboratory, Berwick, Pennsylvania; D. Otis, Clemson University, South Carolina; J. Pojar, British Columbia Ministry of Forests, Smithers; C. St. Claire, University of Alberta, Edmonton; I. Stirling, Canadian Wildlife Service, Edmonton, Alberta; K. W. Stewart, University of Manitoba, Winnipeg; J. Thomson, University of Toronto, Ontario; V. Vickery, McGill University, Montreal; M-A. Villard, Université de Moncton, New Brunswick; R. Wassersug, Dalhousie University, Halifax, Nova Scotia; M. Wheatley, Nunavut Wildlife Management Board, Iqaluit.

I am also indebted to Gary McNulty, President of the Ottawa Field-Naturalists' Club, and the Club Council for continuing support of the journal; Chairman Ron Bedford and the Publications Committee of the OFNC for editorial encouragement and support, to the Canadian Museum of Nature for access to its library and the facilities at the Natural Heritage Building, 1740 Pink Road, Aylmer, Quebec, and to Joyce for everything else.

FRANCIS R. COOK
Editor

Northern Hawk Owl, *Surnia ulula*, nest on a man-made structure in Alaska
MICHELLE L. REAKOFF, JACK L. REAKOFF, and TIM CRAIG 306

rect identification of nest predators of Northern Sage Grouse, *Centrocercus urophasianus*, using remote sensing cameras MATTHEW J. HOLLORAN and STANLEY H. ANDERSON 308

utumn and winter breeding records for the American Robin, *Turdus migratorius*
THOMAS GARDALI and JENNIFER D. WHITE 311

bservations of Long-tailed Weasel, *Mustela frenata*, hunting behavior in central West Virginia BRIAN W. SMITH, CHRIS A. DOBONY, JOHN W. D. EDWARDS, and W. MARK FORD 313

ggressive interactions of Elk, *Cervus elaphus*, during calving season toward Mule Deer, *Odocoileus hemionus*, in central Colorado ROBERT M. STEPHENS, A. WILLIAM ALLDREDGE, and GREGORY E. PHILLIPS 316

ook Reviews

OLOGY: Trout and Salmon of North America — Bigelow and Schroeder's Fishes of Gulf of Maine — Spring Expedition to the Falkland Islands and Antarctica — Shorebirds of the Yellow Sea: Importance, Threats and Conservation Status — Birds of the World: A Checklist — The Rockfishes of the Northeast Pacific — Cavier: The Strange History and Uncertain Future of the World's Most Coveted Delicacy — Plundering Paradise — Birds of the Untamed West: The History of Birdlife in Nebraska, 1750 to 1875 — All-Weather Hawk Watcher's Field Journal — Firefly Encyclopedia of Reptiles and Amphibians — Enjoying Moths 318

OTANY: Ainsworth and Bisby's Dictionary of the Fungi — Illustrated Flora of British Columbia Volumes 1-8 — Ontario Wild Flowers 328

NVIRONMENT: Remote Sensing for Sustainable Forest Management — Snow Ecology: An Interdisciplinary Examination of Snow-Covered Ecosystem — Seabirds and Atlantic Canada's Ship-Source Oil Pollution — Resource Selection by Animals — Monteverde: Ecology and Conservation of a Tropical Cloud Forest 330

ISCELLANEOUS: Charles Darwin: The Power of Place — John Keast Lord: Materials for a Life — The Emperor of Nature: Charles-Lucien Bonaparte and his World — When the Wild Comes Leaping Up: Personal Encounters with Nature — The Dinosaur Filmography — Paleoimagery, The Evolution of Dinosaurs in Art — Naturalists: A Journal — Women Travellers: A Journal 337

ews and Comment

ie Boreal Dip Net: Newsletter of the Canadian Amphibian and Reptile Conservation Network 7(1) January 2003 — *Froglog*: Newsletter of the Declining Amphibian Populations Task Force (56) — *Point Pelee Natural History News* 3(1) — *Marine Turtle Newsletter* (100) — *Recovery*: An Endangered Species Newsletter (24) — Vancouver Aquarium Leatherback Poster 343

ditor's Report for Volume 116 (2002) 346

ailing date of the previous issue 117(1): 30 September 2003

Articles

Effects of plant cover improvements for nesting ducks on grassland birds
STEPHANE LAPOINTE, LUC BELANGER, JEAN-GIROUX, and BERNARD FILLION

Winter bird use of urban and rural habitats in Ontario PAUL G. R. SMITH

Field identification of the mice *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* in central New York ERWIN STEWART LINQUIST, CHARLES F. AQUADRO, DEEDRA MCCLEARN, and KEVIN J. MCGOWAN

Assessing an American Marten, *Martes americana*, reintroduction in Vermont
TRINA L. MORUZZI, KIMBERLY J. ROYAR, CLAYTON GROVE, ROBERT T. BROOKS, CHRISTOPHER BERNIER, FRANK L. THOMPSON, JR., RICHARD M. DEGRAAF, and TODD K. FULLER

Seasonal dynamics and defoliation impact on herbage yield in aspen boreal habitats of Alberta NOBLE DONKOR, MOSES OKELLO, ROBERT HUDSON, and EDWARD W. BORK

Patterns of nestling feeding in Harris's Sparrows, *Zonotrichia querula*, and White-crowned Sparrows, *Z. leucophrys*, in the Northwest Territories, Canada CHRISTOPHER J. NORMENT

The shoreline fringe forest and adjacent peatlands of the southern central British Columbia coast ERIC G. LAMB and WILLIAM MEGILL

Space and habitat use by male and female Raccoons, *Procyon lotor*, in Kansas
JAN F. KAMLER and PHILIP S. GIPSON

Sandhill Cranes, *Grus canadensis*, nesting in the Yorkton wetland complex, Saskatchewan ANN M. BURKE

Physical condition of an animal using as an example the Common Eider, *Somateria mollissima* ARMAUD J. CABANAC

Phenotype variation in skull size and shape between Newfoundland and mainland populations of North American Black Bears, *Ursus americanus*
JOHN A. VIRGL, SHANE P. MAHONEY, and KIM MAWHINNEY

Food habits of Ermine, *Mustela ermina,* in a forested landscape
MARK A. EDWARDS and GRAHAM J. FORBES

Distribution and conservation of the Harlequin Duck, *Histrionicus histricus*, in Greenland DAVID BOERTMANN

Effects of season of burning on the microenvironment of fescue prairie in central Saskatchewan
G. W. ARCHIBOLD, E. A. RIPLEY, and L. DELANOY

Density and richness of benthic invertebrate populations in the North Sydenham River of southwestern Ontario (1996-2000) compared with those of the St. Clair River (1990-1995) I. W. E. HARRIS C. F. DRURY, R. R. SIMARD, and T. Q. ZHANG

New records of vascular plants in the Yukon Territiory V
WILLIAM J. CODY, CATHERINE E. KENNEDY, BRUCE BENNETT, and JENNIFER STANIFORTH

Notes

Malaxis monophyllos var. *brachypoda*, One-leaved Malaxis, new to the Northwest Territories, Canada WILLIAM J. CODY and VICTORIA JOHNSTON

An occurrence of the Hawkweed-leaved Saxifrage, *Saxifraga hieraciifolia*, in southern British Columbia, and its palaeobotanical implications STUART A. HARRIS

ISSN 0008-3550

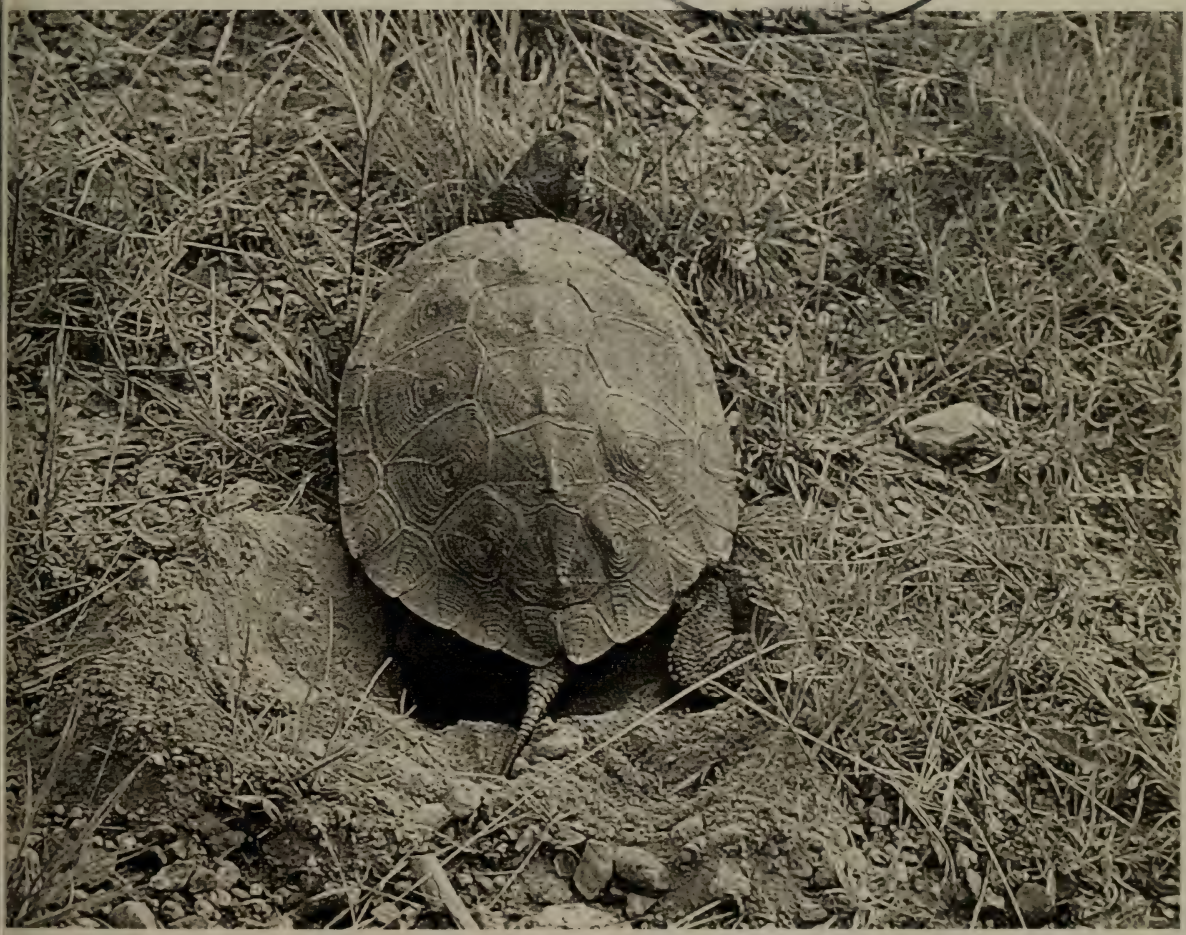
SMITHSONIAN INSTITUTION LIBRARIES
3 9088 01226 6185

DH
1
.213
NH

The CANADIAN FIELD-NATURALIST

Published by THE OTTAWA FIELD-NATURALISTS' CLUB, Ottawa, Canada

SMITHSONIAN
JUL 26 2004
LIBRARIES



Volume 117, Number 3 July–September 2003

The Ottawa Field-Naturalists' Club

FOUNDED IN 1879

Patrons

Her Excellency The Right Honourable Adrienne Clarkson, C.C., C.M.M., C.D.
Governor General of Canada
His Excellency John Ralston Saul, C.C.

The objectives of this Club shall be to promote the appreciation, preservation and conservation of Canada's natural heritage; to encourage investigation and publish the results of research in all fields of natural history and to diffuse information on these fields as widely as possible; to support and cooperate with organizations engaged in preserving, maintaining or restoring environments of high quality for living things.

Honorary Members

Edward L. Bousfield	Bruce Di Labio	John A. Livingston	E. Franklin Pope
Donald M. Britton	R. Yorke Edwards	Stewart D. MacDonald	William O. Pruitt,, Jr.
Irwin M. Brodo	Anthony J. Erskine	Hue N. MacKenzie	Joyce and Allan Reddoch
William J. Cody	John M. Gillett	Theodore Mosquin	Mary E. Stuart
Francis R. Cook	C. Stuart Houston	Eugene G. Munroe	John B. Theberge
Ellaine Dickson	George F. Ledingham	Robert W. Nero	Sheila Thomson

2003 Council

President: Gary McNulty	Ronald E. Bedford	Francis R. Cook	Cendrine Huemer
Vice-President: Mike Murphy	John Cameron	Barbara Gaertner	John Roy
Gillian Marston	Janet Castle	Marcel Gahbauer	Stanley Rosenbaum
Recording Secretary: Ken Alhson	Charlie Clifford	Diane Lepage	Louise Schwartz
Treasurer: Frank Pope	William J. Cody	Karen McLachalan Hamilton	David Smythe
Past President: Eleanor Zurbrigg	Kathy Conlan	David Hobden	Chris Traynor

To communicate with the Club, address postal correspondence to: The Ottawa Field-Naturalists' Club, P.O. Box 35069, Westgate P.O. Ottawa, Canada K1Z 1A2, or e-mail: ofnc@achilles.net.
For information on Club activities telephone (613) 722-3050 or check http//www.achilles.net/ofnc/index.htm

The Canadian Field-Naturalist

The *Canadian Field-Naturalist* is published quarterly by The Ottawa Field-Naturalists' Club. Opinions and ideas expressed in this journal do not necessarily reflect those of The Ottawa Field-Naturalists' Club or any other agency.

We acknowledge the financial support of the Government of Canada toward our mailing cost through the Publication Assistance Program (PAP), Heritage number 09477.

Editor: Dr. Francis R. Cook, R.R. 3, North Augusta, Ontario KOG IR0; (613) 269-3211; e-mail: fcook@achilles.net
Copy Editor: Elizabeth Morton
Business Manager: William J. Cody, P.O. Box 35069, Westgate P.O. Ottawa, Canada KIZ 1A2; (613) 759-1374
Book Review Editor: Roy John, 2175 Emard Crescent, Ottawa, Ontario K1J 6K5; e-mail: roy.john@pwgsc.gc.ca

Associate Editors:	Robert R. Anderson	Paul M. Catling	David Nagorsen
	Charles D. Bird	Brian W. Coad	Donald F. McAlpine
	Robert R. Campbell	Anthony J. Erskine	William O. Pruitt, Jr.

Chairman, Publications Committee: Ronald E. Bedford

All manuscripts intended for publication except Book Reviews should be addressed to the Editor and sent by postal mail. Book-review correspondence should be sent by e-mail or postal mail to Roy John, Book-review Editor.

Subscriptions and Membership
Subscription rates for individuals are $28 per calendar year. Libraries and other institutions may subscribe at the rate of $45 per year (volume). The Ottawa Field-Naturalists' Club annual membership fee of $28 (individual) $30 (family) $50 (sustaining) and $500 (life) includes a subscription to *The Canadian Field-Naturalist*. All foreign subscribers and members (including USA) must add an additional $5.00 to cover postage. The club regional journal, *Trail & Landscape*, covers the Ottawa District and Local Club events. It is mailed to Ottawa area members, and available to those outside Ottawa on request. It is available to Libraries at $28 per year. Subscriptions, applications for membership, notices of changes of address, and undeliverable copies should be mailed to: The Ottawa Field-Naturalists Club, P.O. Box 35069, Westgate P.O. Ottawa, Canada K1Z 1A2. Canada Post Publications Mail Agreement number 40012317. Return Postage Guaranteed. Date of this issue: July–September 2003.

COVER: Wood Turtle, *Glyptemys insculpta*, adult female digging a nest 18 June 2001, at south side of River Denys, Invernes County, Cape Breton Island, Nova Scotia, photograph by John Gilhen. See Gräf, Gilhen, and Adams, pages 415-418; and on the same species in Quebec: Walde, Bider, Daigle, Mase, Bourgeois, Jutras, and Titman pages 377-388.

The Canadian Field-Naturalist

Volume 117, Number 3 July–August 2003

Does Removal of Duck Nest Predators Affect the Temporal Patterns of Predation for Simulated Nests of Grassland Songbirds?

Nancy Dion[1,3], Keith A. Hobson[2], and Serge Larivière[1,3,4]

[1] Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2 Canada
[2] Prairie and Northern Wildlife Research Station, Environment Canada, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4 Canada
[3] Delta Waterfowl Foundation, R.R. 1, Box 1, Site 1, Portage La Prairie, Manitoba R1N 3A1 Canada
[4] Current address: Fédération des Trappeurs Gestionnaires du Québec, 1737, rue Champigny Est, Sainte-Foy, Québec G2G 1A6 Canada

Dion, Nancy, Keith A. Hobson, and Serge Larivière. 2003. Does removal of duck nest predators affect the temporal patterns of predation for simulated nests of grassland songbirds? Canadian Field-Naturalist 117(3): 347-351.

We tested whether the temporal patterns of songbird nest predation changed following removal of predators of duck nests in North Dakota, USA, 1995-1996. Overall, 2286 simulated nests were deployed of which 951 were equipped with depredation timing devices that recorded the time of day of nest destruction. Predators destroyed 242 timer nests, and 155 depredation events were recorded. Temporal distribution of predation events was uniform over a 24-h period. However, predator groups, identified by using marks left on modeling clay eggs, depredated nests at different times. Mean times of depredation were 07h41, 12h57, 17h50, and 22h47 for small mammals, ground squirrels, birds, and medium-sized mammals, respectively. Daily depredation events occurred earlier on removal versus non-removal sites. However, within each predator group, there was no difference in depredation times between removal and non-removal sites. We suggest that the difference in time of depredation is caused by the differential importance of each predator group on removal versus removal sites, and thus conclude that removing duck nest predators does not affect temporal foraging patterns of smaller predators.

Key Words: grasslands, nest predation, predator control, songbirds, timing devices, waterfowl.

In North American grasslands, agricultural expansion and resultant habitat fragmentation have led to increased nest predation rates and have caused declines in numerous populations of ground-nesting birds (Ricklefs 1969; Klett et al. 1988). Consequently, much effort is devoted to mitigate predation of bird nests. Management practices typically involve restoration or conservation of nesting habitats (McKinnon and Duncan 1999), or more intensive methods of predator management such as predator control (Garretson et al. 1996). Most often, predator control is implemented to enhance nest success of economically important avian groups such as waterfowl (Sargeant et al. 1995), or upland game birds (Chessness et al. 1968).

The impact of removing carnivores on the abundance of smaller predators is unknown. In some areas, removing larger predators led to trophic effects and the increased abundance of smaller predators (Palomares et al. 1995). During short-term (one season) predator control, nest success of grassland songbirds was not affected by removal of larger predators (Dion et al. 1999), possibly because of compensatory predation on songbird nests by smaller predators such as ground squirrels (*Spermophilus*) or smaller mammals (Dion et al. 2000). The compensatory response was suggested because both groups of small predators depredate nests in more open habitats on sites where predators were removed, possibly because they perceived reduced predation risk (Lima and Dill 1990) or because vulnerable animals occupying more open habitats experienced improved survival and consequently could depredated more nests. Herein, we compare the daily patterns of depredation of simulated songbird nests between sites with and without removal of predators to test whether predators of songbird nests displayed different temporal foraging patterns.

Study Area and Methods

We conducted this study during the breeding seasons of 1995 and 1996 as part of a larger study on the .effects of predator removal on the nesting success of songbirds in the grasslands of eastern (48° N, 98° W) North Dakota, USA. This region has little relief and is dominated by small grain agriculture. Wetlands and fields enrolled under the Conservation Reserve Program and Water Bank Program, as well as Waterfowl Production Areas occur throughout the area (Garretson et al. 1996).

Each year, we chose eight sites (all sites > 6 km apart) that possessed numerous potholes and with 10-30% of their surface as perennial grasslands. Each site was 41 km^2 in size, and was randomly assigned as "removal" or "non-removal". Removal sites were subjected to intensive predator trapping while non-removal sites were left untreated (Garrettson et al. 1996). Predator removal was performed from March through July, using similar removal methods (box-traps, snares, leghold traps, and shooting) on all removal sites. Red Fox (*Vulpes vulpes*), Striped Skunk (*Mephitis mephitis*), Raccoon (*Procyon lotor*), and America Badger (*Taxidea taxus*) were targeted for removal.

Within each site, we established three 500-m transects for the placement of simulated nests. All transects were in contiguous areas of grassland without wetlands or shelterbelts and were placed in grasslands (mostly Conservation Reserve Program fields) of similar vegetative structure. Distance between any two transects was >1.6 km.

Simulated nests consisted of a commercial wicker nest (9 cm in diameter and 5 cm deep) lined with grass and other local vegetation. In each nest, we placed one Japanese Quail (*Coturnix japonica*) egg and one painted modeling clay egg. Modeling clay eggs were used to help detect and identify predators based on beak and tooth marks (Major 1991; Bayne et al. 1997) because predators cannot be identified from nest remains (Larivière 1999). We wore rubber boots and gloves while handling nests and eggs to reduce human scent.

We deployed nests on the ground at 20-m intervals and at random distances (5-25 m) from transect lines, alternating sides for consecutive nests. Twenty-five nests were deployed per transect for a total of 75 nests per site. Simulated nests were exposed for 12 days to mimic a typical songbird incubation period (Rudnicky and Hunter 1993).

We visited simulated nests every four days and removed destroyed nests from transects. We considered a nest destroyed if at least one egg was missing or destroyed or if any marks were left on the modeling clay eggs. Each year we conducted two trials (early June and early July) to mimic the peak nesting and renesting period of grassland songbirds in North Dakota (Stewart and Kantrud 1972).

To identify predators, we compared width of teeth marks to measurements of 10-15 skulls of each species of small mammals and ground squirrels from the Biology Museum, University of Saskatchewan. Because many species have overlapping tooth patterns (N. Dion, unpublished data), we grouped predators according to ecological relatedness: small mammals (*Peromyscus* spp., *Microtus* spp., *Clethrionomys* spp.), ground squirrels, medium-sized carnivores (Striped Skunk, Raccoon, American Badger, Red Fox), birds (primarily Sedge Wren, *Cistothorus platensis*, and Brown-headed Cowbirds, *Mlolothrus ater*). Modeling clay eggs left without marks or with confusing marks were classified as being destroyed by unknown predators.

At each nest, we positioned one egg on a timing device (modified from Ball et al. 1994). Timing devices consisted of stopwatch glued to the sides of a wicker nest (to provide stability of the clock), with an egg placed on the stop switch. Clocks were adjusted to current time, and removal of the egg from the switch (following depredation) stopped the clock and recorded the time of depredation. Because the number of timers was smaller than the total number of nests, we placed timers at the last 20 nests of each transect.

Times of depredation were compared using circular statistics. We first tested data sets for uniformity using Rayleigh's uniformity test, then compared samples using Watson's F-test for circular means.

Results

Trappers removed 1166 and 908 medium-sized predators from the experimental sites in 1995 and 1996, respectively (Garretson et al. 1996). During both years, trappers removed primarily Raccoon (42%), Striped Skunk (31%), and Red Fox (24%). American Badger and American Mink (*Mustela vison*) comprised the remaining 3%. Because predator densities were not monitored, it is unknown to what degree removal operations affected predator densities or communities. However, because of the high effort and number of animals removed, we suspect most of the resident target animals were removed during trapping.

We monitored nest fate for 1125 and 1161 nests in 1995 and 1996, respectively. Of those, timers were placed at 951 nests (42% of monitored nests), and 242 were depredated (25%, n = 951). Timers recorded 155 depredation events (64%). Because of the small sample of nests, we could not test for effects of year or trial. Instead, we focused on the more important effects of predator type and treatment (removal versus non-removal sites).

Depredation events were distributed uniformly throughout the day (Rayleigh test of uniformity, P = 0.22; Figure 1A). However, specific predator groups did not prey on nests uniformly throughout the day (medium mammals, $P = 0.03$; ground squirrels, $P < 0.01$; small mammals, $P = 0.10$; birds, $P = 0.10$). Mean depredation time differed between all groups (Watson's F-tests for two-circular samples, multiple comparisons adjusted with Bonferonni correction, all $F > 8.50$, all $P < 0.01$). Mean depredation times averaged 07:41, 12:57, 17:50, and 22:47 for small mammals, ground squirrels, birds, and medium-sized mammals, respectively (Figure 1B, C, D, E).

Time of nest destruction was evenly distributed throughout the day on non-removal sites (Rayleigh test of uniformity, $P = 0.88$), but not on removal sites ($P = 0.02$). Mean depredation time differed (Watson's

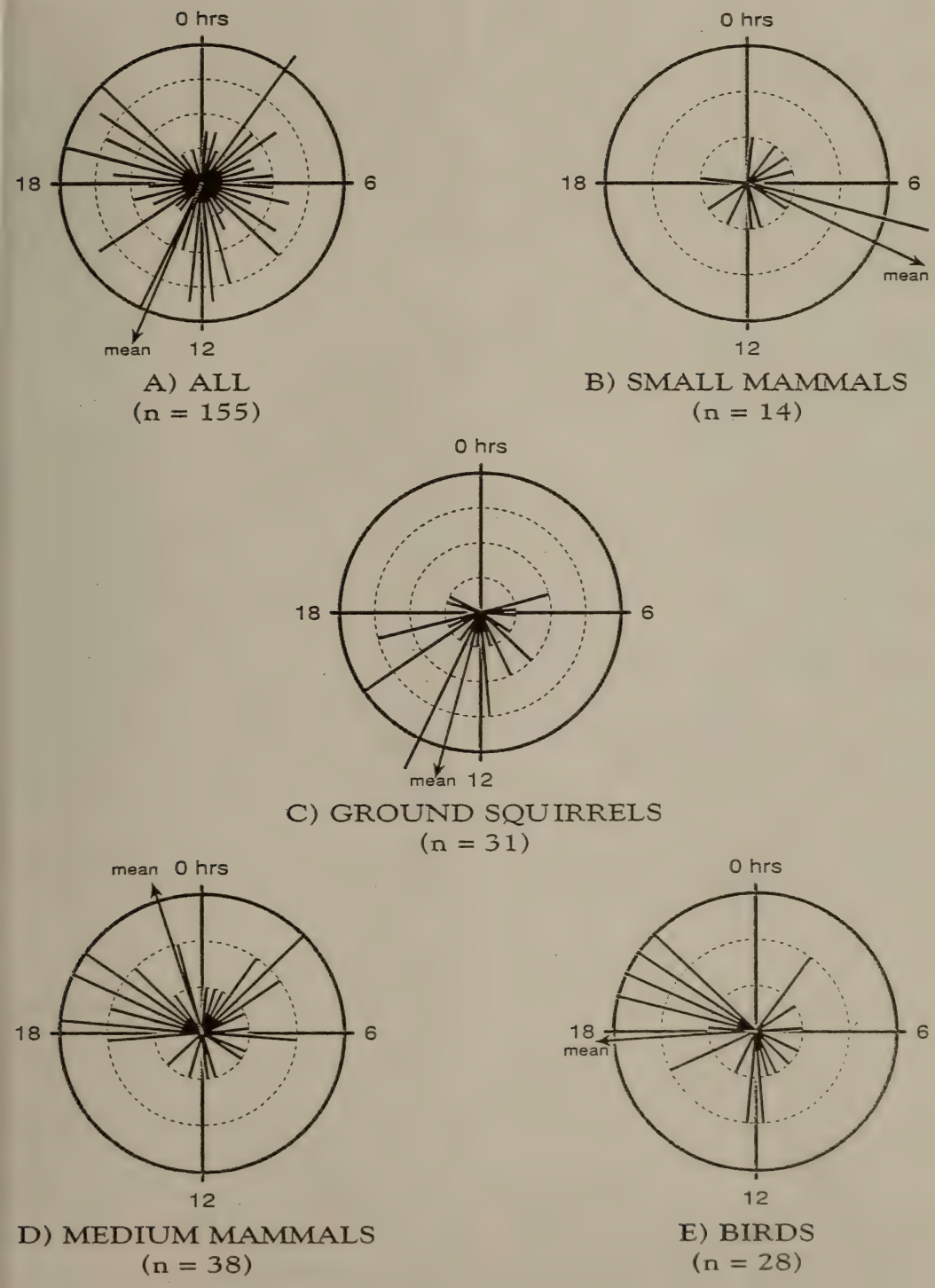
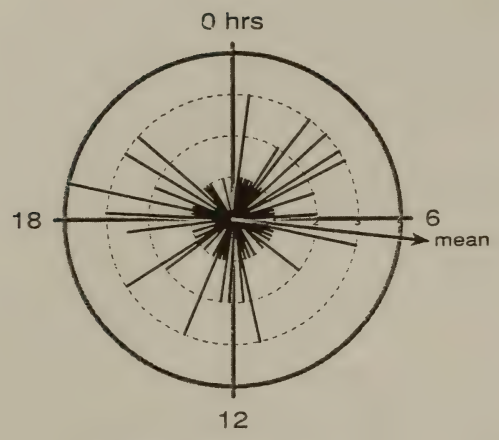


FIGURE 1. Temporal patterns of depredation by various predators of simulated nests of grassland songbirds in north-eastern North Dakota, 1995-1996. *n* indicates the number of nests. Concentric dotted lines equal one predation event. Dark lines indicate time of predation events.



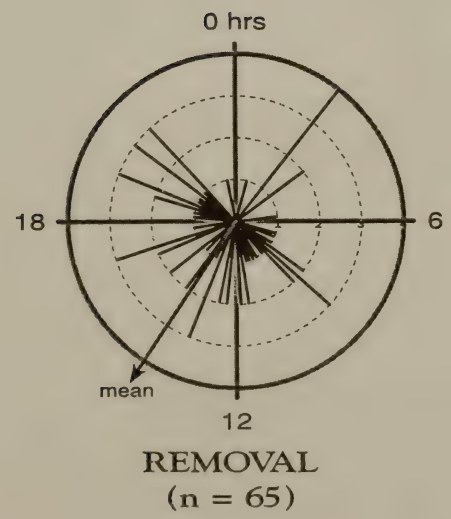


Figure 2. Temporal patterns of depredation of simulated nests of grassland songbirds on sites where duck nest predators were removed (removal) and not removed (non-removal) in northeastern North Dakota, 1995-1996. *n* indicates the number of nests. Concentric dotted lines equal one predation event. Dark lines indicate time of predation events.

F-test for two circular means, $F = 5.22$, $P = 0.02$) between nests depredated on removal sites (mean = 14:13, $n = 65$) and nest depredated on non-removal sites (mean = 06:26, $n = 90$; Figure 2).

We tested whether depredation times differed for each predator group following removal of duck nest predators. Using Bonferroni corrections to compensate for multiple comparisons, we considered values <0.0125 as significant. Consequently, we detected no differences in depredation times between removal and non-removal sites for nests depredated by birds ($F = 1.37$, $P = 0.25$, mean = 17:50, $n = 28$), small mammals ($F = 0.02$, $P = 0.88$, mean = 07:41, $n = 14$), ground squirrels ($F = 0.06$, $P = 0.81$, mean = 12:57, $n = 31$), or medium mammals ($F = 3.76$, $P = 0.06$, mean = 22:47, $n = 38$).

Discussion

We did not detect differences in depredation times between removal and non-removal sites for any of the predator groups. Previously, we showed that predators at lower trophic levels (e.g., ground squirrels and small mammals) depredated nests with different vegetative characteristics, suggesting a spatial response to the removal of predators at higher trophic levels (Dion et al. 2000). Similar depredation times between removal and non-removal sites for each individual predator group suggest that differences observed between areas were caused by the relative importance of each predator group (Dion et al. 1999). Specifically, ground squirrels were more important as predators on removal sites, and their mean predation time was in midday (12:57), which would shift the mean depredation time for removal sites toward early afternoon, a pattern that corresponds with what we observed (Figure 2).

The study of temporal patterns of nest predation is still relatively new (Ball et al. 1994) and hence few data are available for comparison (Ball et al. 1994; Picman and Schmirl 1994; Bayne and Hobson 1997; Larivière and Messier 2001). With the development of more sophisticated methods such as video cameras to monitor bird nests (e.g., Pietz and Granfors 2000), new insights into the behavior of nest predators will be gained. Although our sample of nests with timers was limited, our study emphasized the usefulness of timer nests in examining the nature and dynamics of predation on grassland songbird communities. Combined with the use of clay eggs or photographic means of recording predators, timer nests should be encouraged as a refinement to the more common use of artificial nests to study nest predation.

Acknowledgments

This study was funded by the Delta Waterfowl Foundation. Additional funding was obtained from the Canadian Wildlife Service through an operating grant to K. A. Hobson and from the University of

Saskatchewan through a graduate scholarship to N. Dion. Logistic support during manuscript preparation was provided by the Institute for Wetland and Waterfowl Research (Ducks Unlimited Inc.), and Delta Waterfowl Foundation. We thank S. Fischer, C. McLaren, N. Kemptf, W. Johnson, M. Holt, M. Schmoll, J. Kreilich, M. Hoff, B. Luse, K. Pontesso, and J. Jordan for field assistance. We are grateful to F. C. Rohwer and J. Scarth who encouraged our participation in this project. C. Birchler and J. Gandy helped with the figures. D. Granfors reviewed an earlier draft of this manuscript.

Literature Cited

Ball, J. I., R. J. Gazda, and **D. B. McIntosh.** 1994. A simple device for measuring survival time of artificial nests. Journal of Wildlife Management 58: 793-796.

Bayne, E. M., and **K. A. Hobson.** 1997. Temporal patterns of predation on artificial nests in the southern boreal forest. Journal of Wildlife Management 61: 1227-1234.

Bayne, E. M., K. A. Hobson, and **P. Fargey.** 1997. Predation on artificial nests in relation to forest type: contrasting the use of quail and plasticine eggs. Ecography 20: 233-239.

Chessness, R. A., M. M. Nelson, and **W. H. Longley.** 1968. The effect of predator removal on pheasant reproductive success. Journal of Wildlife Management 32: 683-697.

Dion, N., K. A. Hobson, and **S. Larivière.** 1999. Effects of removing duck nest predators on nesting success of grassland songbirds. Canadian Journal of Zoology 77: 1801-1806.

Dion, N., K. A. Hobson, and **S. Larivière.** 2000. Interactive effects of vegetation and predators on nesting success of grassland songbirds. Condor 102: 629-634.

Garretson, R. P., F. C. Rohwer, J. M. Zimmer, B. J. Mense, and **N. Dion.** 1996. Effects of mammalian predator removal on waterfowl and non-game birds in North Dakota. Transactions of North American Wildlife Natural Resources Conference 61: 94-101.

Klett, A. T., T. L. Shaffer, and **D. H. Johnson.** 1988. Duck nest success in the prairie pothole region. Journal of Wildlife Management 52: 431-440.

Larivière, S. 1999. Reasons why predators cannot be inferred from nest remains. Condor 101: 718-721.

Larivière, S., and **F. Messier**. 2001. Temporal patterns of predation of duck nests in the Canadian prairies. American Midland Naturalist 146: 339-344.

Lima, S. L., and **L. M. Dill.** 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal Zoology 68: 619-640.

Major, R. E. 1991. Identification of nest predators by photography, dummy eggs, and adhesive tape. Auk 108: 190-195.

McKinnon, D. T., and **D. C. Duncan.** 1999. Effectiveness of dense nesting cover for increasing duck production in Saskatchewan. Journal of Wildlife Management 63: 382-389.

Palomares, F., P. Gaona, P. Ferreras, and **M. Delibes.** 1995. Positive effects on game species of top predators by controlling smaller predator populations: an example with lynx, mongooses, and rabbits. Conservation Biology 9: 295-305.

Picman, J., and **L. M. Schmirl.** 1994. A camera study of temporal patterns of nest predation in different habitats. Wilson Bulletin 106: 456-465.

Pietz, P. J., and **D. A. Granfors.** 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management 64: 71-87.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contribution to Zoology 9: 1-48.

Rudnicky, T. C., and **M. L. Hunter.** 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. Journal of Wildlife Management 57: 358-364.

Sargeant, A. B., M. A. Sovada, and **T. L. Shaffer.** 1995. Seasonal predator removal relative to hatch rate of duck nests in waterfowl production areas. Wildlife Society Bulletin 23: 507-513.

Stewart, R. E., and **H. A. Kantrud.** 1972. Population estimates of breeding birds in North Dakota. Auk 89: 766-788.

Received 30 October 2000
Accepted 29 March 2004

Characteristics of Early-Winter Caribou, *Rangifer tarandus caribou,* Feeding Sites in the Southern Purcell Mountains, British Columbia

TREVOR A. KINLEY[1,2], JOHN BERGENSKE[3], JULIE-ANNE DAVIES[4], and DAVID QUINN[5]

[1]Sylvan Consulting Ltd., RR5 3519 Toby Creek Road, Invermere, British Columbia V0A 1K5 Canada
[2]Corresponding author: e-mail: sylvan@rockies.net
[3]Box 84, Skookumchuck, British Columbia V0B 2E0 Canada
[4]465 Creston Street, Kimberley, British Columbia V1A 2M4 Canada
[5]2410 DeWolfe Street, Kimberley, British Columbia V1A 1P9 Canada

Kinley, Trevor A., John Bergenske, Julie-Anne Davies, and David Quinn. 2003. Characteristics of early-winter Caribou, *Rangifer tarandus caribou,* feeding sites in the southern Purcell Mountains, British Columbia. Canadian Field-Naturalist 117(3): 352-359.

Mountain Caribou are a rare ecotype of Woodland Caribou (*Rangifer tarandus caribou*) inhabiting the high-snowfall region of southeastern British Columbia, and are defined by their late-winter reliance on arboreal hair lichen of the genus *Bryoria*. During early winter, there is considerable variation in habitat use among populations. We snow-trailed Caribou in the southern Purcell Mountains during early winter to determine foraging patterns for the Purcell population. When snow was ≤51 cm deep, Caribou fed on Grouseberry (*Vaccinium scoparium*), the terrestrial lichen *Cladonia*, and arboreal lichens of the genus *Bryoria*. When snow was ≥62 cm deep, they ate exclusively arboreal lichens. In both periods, Caribou ate arboreal lichen from essentially every downed tree or branch encountered and fed with a higher intensity at downed trees than standing trees. During the low-snow period, Caribou fed at fewer trees but used those with greater lichen abundance, and fed more intensively at each, compared to the deep-snow period. In comparison to trees occurring on the foraging path but at which Caribou did not feed, those from which arboreal lichen was foraged intensively were of larger diameter, had greater lichen abundance, and were more likely to be Subalpine Fir (*Abies lasiocarpa*) or Engelmann Spruce (*Picea engelmannii*) and less likely to be Whitebark Pine (*Pinus albicaulis*), Lodgepole Pine (*P. contorta*) or Alpine Larch (*Larix lyalli*). The shift in diet between the low-snow and deep-snow periods reflected two modes of foraging within the early winter period, distinct from one another and apparently also distinct from the late-winter season. Management for early-winter habitat will require retention of some commercially significant forest across extensive areas, both near the subalpine forest – subalpine parkland ecotone and lower in the subalpine forest.

Key Words: Woodland Caribou, *Rangifer tarandus caribou*, habitat, early winter, Grouseberry, *Vaccinium scoparium*, lichen, *Bryoria*, Purcell Mountains, British Columbia.

The ecotype of Woodland Caribou (*Rangifer tarandus caribou*) occurring in the wetter portions of southeast British Columbia, northern Idaho and northeastern Washington is known in British Columbia as Mountain Caribou (Heard and Vagt 1998) or Mountain/Arboreal Caribou (Edmonds 1991). This ecotype has a population of 1900 distributed in 13 populations (Hatter et al. 2002*). It is on British Columbia's red list, indicating it is "imperilled provincially because of extreme rarity or because of some factor(s) making it especially vulnerable to extinction" (Conservation Data Centre 2003*). It is also included with some populations of another ecotype on Canada's threatened list (Committee on the Status of Endangered Wildlife in Canada 2002*), and is listed as endangered in the USA (United States Fish and Wildlife Service 1994*). Mountain Caribou differ from other Woodland Caribou ecotypes in being almost entirely dependent upon arboreal hair lichen (mainly horsehair lichens, especially *Bryoria* spp.) rather than terrestrial lichen for late-winter food, because of the extremely deep snowpacks at higher elevations in this region (Edwards et al. 1960; Stevenson and Hatler 1985). Deep snow in late winter makes cratering for terrestrial lichen or other ground-based foods difficult or impossible. However, deep snow also provides the necessary lift to reach *Bryoria*, which is more abundant >2 m above the ground (Rominger and Oldemeyer 1990; Goward 1998). This food source is generally abundant only on old conifer trees (Goward 1998), which is one of the reasons that Mountain Caribou are considered to be reliant on oldgrowth forest. These forests also have potentially high timber values.

Early-winter foraging differs from that of late winter in several respects. Until snowpacks deepen and consolidate sufficiently to allow Caribou to readily obtain arboreal lichen from standing trees, they also (1) make use of arboreal lichen available as litterfall on the snow's surface or on windthrown trees or branches (Stevenson et al. 2001), and (2) in many locations crater through snow to eat forbs such as Foamflower (*Tiarella* spp.) and Mitrewort (*Mitella* spp.), terrestrial lichens including Lungwort (*Lobaria pulmonaria*), various pelt lichens (*Peltigera* spp.) and Cladonia (*Cladonia* spp.), shrubs, especially Falsebox (*Pachistima myrsinites*), Bunchberry (*Cornus canadensis*), Twinflower (*Linnaea borealis*) and various huckleberries (*Vaccinium* spp.),

* See Documents Cited section.

and graminoids (Edwards and Ritcey 1960; Freddy 1974; Bloomfield 1979; Antifeau 1987; Simpson et al. 1987; Rominger and Oldemeyer 1990; McLellan and Flaa 1993*; Mowat et al. 1998*; Terry et al. 2000; Stevenson et al. 2001). The early-winter season typically lasts from November through mid-January, and is associated with shifts to lower elevations (Stevenson et al. 2001; Apps et al. 2001). In sum, winter seasons for Mountain Caribou include early winter up to about mid-January, during which forage includes both arboreal lichen and ground-based foods at low to moderate elevations, then late winter when deep, consolidated snowpacks at higher elevations provide sufficient lift to more readily reach the abundant arboreal lichens higher in trees.

The southern Purcell Mountains population is at the southeastern limit of remaining Mountain Caribou distribution. This population has recently declined to about 20 animals (Kinley and Apps 2001) and is isolated. Habitat models for the southern Purcell Mountains have been created at the landscape and stand scale (Apps and Kinley 2000*; Kinley and Apps 2000*), providing guidance for habitat protection based on characteristics of forest stands and topography. The models indicate that the average downward movement during early winter in the southern Purcell Mountains is slight, with most activity occurring in forests close to treeline. However, those models were at spatial scales coarser than those at which detailed foraging decisions are made, so many of the variables used may have been surrogates for the attributes Caribou selected. Snow-trailing investigations of Mountain Caribou have been conducted in some parts of British Columbia to determine foraging strategies at fine spatial scales (McLellan and Flaa 1993*; Ashcroft 1997*; Mowat et al. 1998*; Terry et al. 2000). However, these studies may not be applicable in the southern Purcell Mountains due to differences in physiography, climate and vegetation, and the considerable variation in early-winter habitat use employed by Mountain Caribou (Terry et al. 2000, Apps et al. 2001, Stevenson et al. 2001). Given the conservation concerns for Mountain Caribou generally and the southern Purcell Mountains population in particular, a better understanding of habitat use patterns would be beneficial. Therefore, we conducted a snow trailing investigation during early winter in the southern Purcell Mountains to determine local patterns of Caribou feeding-site selection.

Study Area

Within our 5000-km^2 study area, physiography ranges from subdued ridges to high ridges and mountains, with elevations of 530 to 2850 m. The climate of this area is somewhat drier than the rest of Mountain Caribou range (Curran et al. 1992), but there is a general trend within the study area towards increasing precipitation from northeast to southwest, and from lower to higher elevations. In areas with less precipitation, the trend in climax tree species is: Douglas-fir (*Pseudotsuga menziesii*) at elevations below about 1150 m; hybrid White Spruce (*Picea glauca* × *engelmannii*) to about 1600 m; a closed-canopy forest of Engelmann Spruce (*P. engelmannii*) and Subalpine Fir (*Abies lasiocarpa*) to about 2100 m (hereafter "subalpine forest"); open stands of Subalpine Fir, Whitebark Pine (*Pinus albicaulis*) and Alpine Larch (*Larix lyalli*) to about 2600 m ("subalpine parkland"); then alpine tundra over about 2600 m (Curran et al. 1992). In moister areas, the subalpine forest occurs at elevations between about 1550 and 1950 m, and land below it has climax forests of Western Redcedar (*Thuja plicata*) and Western Hemlock (*Tsuga heterophylla*). Lodgepole Pine (*Pinus contorta*) is a common fire-successional species in all forested zones. It typically occurs in pure stands when young, but often persists in mixed stands at climax.

Methods

We located radiocollared Caribou (n = 10) from 10 November 1998 through 5 January 1999 using telemetry-equipped aircraft. This was on a nominal weekly schedule although inclement weather made the actual schedule variable. On the first day following each flight we randomly selected one of the radiocollared animals, then approached that animal or the group in which it occurred from the ground until the first trail was observed in the snow. We followed the trail in the direction of Caribou travel unless it appeared to have been made that day, in which case we traveled in the reverse direction to avoid displacing the Caribou. Individual Caribou seldom diverged far from the group's trail but when this occurred, we followed the most distinct path (presumably having been made by the greatest number of animals). We recorded snow depth and Caribou sinking depth at the first track encountered and every 500 m thereafter, with distances measured using a hip-chain. We used the difference between snow depth and sinking depth to determine the lift provided by the snowpack. Along the trail, we recorded all feeding sites, which we defined as either a crater dug by Caribou to reach ground-based foods, or a tree (standing or downed) or downed branch from which Caribou had eaten arboreal lichen. We noted the distance of each feeding site from the previous one, and classified each as being of either a single type (arboreal lichen on a standing tree, arboreal lichen on a downed tree, arboreal lichen on a downed branch, shrubs, forbs, or terrestrial lichen), or a combination of types (shrub-terrestrial lichen, standing tree-shrub, or standing tree-terrestrial lichen). Terrestrial feeding sites were evident as craters in the snow, usually with bite marks evident on the vegetation and often with fragments of broken vegetation present on the snow or ground surface. Due to the structure of arboreal hair lichens and the breakage of arboreal lichens even without foraging activity, it was usually not possible to determine with certainty whether bites had been

taken from arboreal lichen clumps, so trampling of the snow within reach of them was assumed to correspond to feeding events. For standing-tree and downed-tree sites, we classified the tree according to species, arboreal lichen abundance (ranging from estimated values of 0 to >625 g of lichen within 4.5 m of the ground, on a 0 to 5 scale; Armleder et al. 1992), whether live or dead, and diameter at breast height (1.3 m above ground). For feeding sites of all types, we coded the intensity of feeding (McLellan and Flaa 1993*) as 2 (low; two or fewer steps off of trail toward feeding site), 3 (moderate; <50% of area around tree, branch or crater tracked and individual hoof prints visible) or 4 (high; >50% of area trampled). In addition, we recorded all downed branches or downed trees at which feeding had not occurred (code 1) if they were within 1 m of the trail centerline and were exposed above the snow. We also classified the first unused standing tree within 1 m of the trail every 200 m. We continued trailing as long as light permitted each day. One of the remaining groups having a radiocollared animal was chosen at random for tracking on the following days for up to three days after each radiotelemetry flight, after which movements since the date of aerial telemetry made locating Caribou impractical. All trailing occurred within subalpine forest and subalpine parkland, and was within mature or oldgrowth forest.

Radiocollared Caribou usually occurred in groups (≤4), so the identity and sex of the Caribou making the trail we followed were generally not known and we did not stratify the analysis by sex. We summarized use of each feeding type with respect to the earlier versus later portion of our data-collection period to define two distinct foraging periods or foraging modes, then assessed differences in: (1) intensity of arboreal lichen feeding at standing versus downed trees; (2) environmental and feeding measures between the two foraging periods (snow depth, lift, elevation, arboreal lichen abundance, arboreal lichen-feeding intensity, distance between trees on which arboreal lichen feeding occurred, and proportion of days when downed trees were used for arboreal lichen feeding); and (3) tree characteristics between sites where feeding intensity was low and sites where it was moderate to high for all sample days combined (arboreal lichen abundance, tree diameter, tree species, and whether trees were alive or dead). Downed branches were excluded from this latter analysis as they would have had far less lichen than entire trees. Sites at which a combination of feeding types occurred (7% of sites) were excluded from comparisons of feeding intensity. For statistical analyses, we used t-tests for continuous variables, Mann-Whitney U tests for discrete variables on ordinal scales, and chi-square tests for discrete variables on nominal scales.

Results

We completed 20 891 m of trailing on 12 days (153 – 3653 m/day), at elevations of 1560 to 2326 m (mean = 1971 m, SE = 57). Within this, we recorded 816 feeding sites for an average of 25.6 m of travel per feeding site. *Cladonia* was the dominant terrestrial lichen found at feeding sites, and examinations of bite marks suggested feeding was focused on it (i.e., it was not present simply because it had not been eaten). Caribou ate Grouseberry (*Vaccinium scoparium*), which maintains its green foliage in winter, at all but one shrub or shrub-combination site. Heather (*Cassiope mertensiana*, *Phyllodoce empetriformis*, or *P. glanduliflora*) was eaten in combination with *Cladonia* at one site and in combination with Grouseberry at four sites. The species of arboreal lichen on standing or downed trees and downed branches was not recorded in data forms, but field notes indicated that it was almost always *Bryoria* spp., with *Alectoria sarmentosa* constituting <1% or occasionally <5% of the lichen per transect. Feeding occurred at 55 of the 56 downed trees and all 11 downed branches. No additional unused downed trees or branches were observed off transects within sight of observers. Moderate- to high-intensity feeding was recorded more often at downed trees than standing trees (67% versus 25%, $\chi^2 = 617$, $P < 0.001$).

We observed the use of arboreal lichen on standing trees, downed trees and downed branches throughout the sample period (11 November – 06 January), but shrubs and terrestrial lichen were used only between 11 November and 19 November (Table 1). During the earlier period when Caribou fed on both ground-based foods and arboreal lichen, snow depths were shallower (daily averages of 9 – 51 cm) than the later period when they fed exclusively on arboreal lichen (62-198 cm), and lift paralleled this difference (Table 2). Mean elevations were higher during the shallow-snow period than during the deep-snow period (Table 2). During the shallow-snow period, Caribou feeding sites had a greater proportion of trees with high lichen abundance and high-intensity feeding, and trees on which foraging occurred were farther apart, in comparison to the exclusively arboreal lichen-foraging period (Table 2). There was no difference between the two periods in the proportion of days on which Caribou fed on downed trees or branches (Table 2). The mean number of Caribou per group trailed was similar between the two periods (2.4 for the ground-foraging period, 2.1 for the exclusively arboreal lichen-foraging period; $t = 0.49$, $P = 0.635$).

In comparison to unused standing trees, trees with moderate to high feeding intensity had greater lichen loads, larger diameter, and were more often Subalpine Fir or Engelmann Spruce and less often Alpine Larch, Whitebark Pine or Lodgepole Pine (Table 3). There was no difference in whether trees were alive or dead (Table 3).

TABLE 1. Occurrences of each feeding type at Mountain Caribou forage sites during early winter, southern Purcell Mountains, British Columbia, 1998-1999.

	Percentage of Feeding Sites		
Feeding Type	11 November – 19 November (n = 390)	20 November – 06 January (n = 426)	Total (n = 816)
Shrub	29.5	0.0	14.1
Terrestrial lichen	0.3	0.0	0.1
Shrub + terrestrial lichen	10.8	0.0	5.1
Arboreal lichen on standing tree	50.8	89.0	70.7
Arboreal lichen on standing tree + shrub	3.6	0.0	1.7
Arboreal lichen on standing tree + terrestrial lichen	0.3	0.0	0.1
Arboreal lichen on downed tree	4.4	8.9	6.7
Arboreal lichen on downed branch	0.5	2.1	1.3

The data are undoubtedly autocorrelated to some degree due to many feeding sites per day being the result of a single animal or group of animals, and being close to each other. However, four to seven feeding types were observed per day on all but one day, so animals did appear to make feeding-type choices on a continual basis.

Discussion

Two modes of foraging were apparent. When snow was shallow, Caribou used Grouseberry and *Cladonia* located under the snow and also fed intensively on arboreal lichen at a few trees having high lichen loads. When snow was deeper and provided greater lift, Caribou fed exclusively on arboreal lichen, typically with low-intensity feeding sessions at more trees having lower lichen abundance than those used earlier. When the green and presumably higher-protein Grouseberry was more available due to shallow snow, lichen from standing trees would have been less available due to the lack of lift. At that time, Caribou may have employed a strategy of searching for Grouseberry and restricting their use of arboreal lichen to when they happened upon either downed trees or standing trees with unusually high lichen loads. This approach would be consistent with the greater distance between feeding sites recorded here and noted by Simpson et al. (1987) prior to the onset of an exclusively arboreal lichen diet. In contrast, when snow was deep, arboreal lichen was the only available food and occurred in varying amounts on virtually every tree, so Caribou may have shifted strategies to inspect more trees in an effort to locate better lichen patches. In both cases, Caribou fed at essentially all windthrown trees and

TABLE 2. Snow and foraging characteristics on early-winter days when Mountain Caribou fed exclusively on arboreal lichen versus days when they fed on both arboreal lichen and ground-based foods (shrubs or terrestrial lichen), southern Purcell Mountains, British Columbia, 11 November 1998 – 6 January 1999.

	Foraging Mode					
	Arboreal Lichen & Ground Forage (≤19 November)		Arboreal Lichen Only (≥20 November)			
Measure	n	value	n	value	Test	*P*
Mean snow depth (cm) +/- SE	27	32 (3)	34	143 (6)	*t*	< 0.001
Mean lift (snow depth – sinking depth [cm]) +/- SE	27	9 (2)	34	109 (7)	*t*	< 0.001
Elevation (m) at midpoint of daily trailing segment +/- SE	5	2100 (84)	7	1878 (59)	*t*	0.049
Arboreal lichen abundance (5:4:3:2:1:0[1]) at standing-tree sites (%)	198	0:35:43:20:1:0	379	0:7:48:41:4:0	*U*	< 0.001
Feeding intensity (4:3:2[2]) at standing tree sites (%)	211	7:40:53	376	2:15:83	*U*	< 0.001
Mean distance between arboreal lichen sites[3] (m) +/- SE	225	52 (7)	440	21 (3)	*U*	< 0.001
Days downed trees used: days not observed to be used	5	4:1	7	5:2	χ^2	0.735

[1] based on Armleder et al. (1992)
[2] 4 = high, 3 = moderate, 2 = low
[3] standing tree, downed tree or downed branch sites

TABLE 3. Characteristics of standing trees where Caribou feeding did not occur versus standing trees where feeding intensity was moderate to high, southern Purcell Mountains, British Columbia, 11 November 1998 – 6 January 1999.

Measure	Feeding Intensity		Test	*P*
	None (n = 94)	Moderate-High (n = 136)		
Arboreal lichen abundance 5:4:3:2:1:0[1] (%)	0:6:28:35:28:3	0:29:51:21:0:0	*U*	< 0.001
Mean tree diameter (cm) +/- SE	25.2 (1.3)	29.5 (1.3)	*U*	0.045
Tree species Bl:Se:Pl:Pa:La[2] (%)	46:15:20:10:10	74:23:2:2:0	χ^2	< 0.001
Live trees: dead trees (%)	88:12	85:15	χ^2	0.420

[1] based on Armleder et al. (1992)
[2] Bl = Subalpine Fir, Se = Engelmann Spruce, Pl = Lodgepole Pine, Pa = Whitebark Pine, La = Alpine Larch

branches encountered, used downed trees more intensively than they did standing trees, and used them to the same degree in the low-snow and deep-snow periods. Consistent with our results, Rominger and Oldemeyer (1990) found the diet to shift away from ground-based food sources when snow depth exceeded 50 cm.

The simplest explanation for the patterns we observed is that it reflected the typical annual shift from a mixed early-winter diet to an arboreal lichen-only late-winter diet, with the early date of the shift resulting from the 50-cm snowpack we observed in mid-November being four weeks ahead of normal at 1930 m elevation in our study area (British Columbia Ministry of Environment, Lands and Parks Snow Survey Bulletin, 01 February 2000, unpublished data). However, the same snow data suggest that even the normal date for that snowpack (the threshold preventing ground-feeding) in the southern Purcell Mountains would be roughly a month earlier than the typical late-winter start date of mid-January. The same is true for the Revelstoke population of Mountain Caribou, in which the 50-cm mark is surpassed on early-winter ranges in early December (Stevenson et al. 2001), a month before the ascent to late-winter ranges (Apps et al. 2001). Furthermore, animals we trailed moved downslope to an elevation of <1900 m when they began using only arboreal lichen. This is considerably below either the early-winter or late-winter averages reported for this study area (about 1950 to 2150 m; Apps and Kinley 2000*), and is counter to the normal pattern of ascending from early-winter to late-winter habitats reported both for Mountain Caribou generally (Apps et al. 2001; Stevenson et al. 2001) and in the southern Purcell Mountains specifically (Apps and Kinley 2000*). Finally, arboreal lichen from windthrown trees and branches continued to be well-used throughout our study period. Thus, the data suggest that both the mixed-foraging strategy and that of eating only arboreal lichen (with considerable emphasis on downed trees and branches) are part of the early-winter foraging pattern for Caribou in the southern Purcell Mountains. This implies that early winter is characterized by considerable intra-season variability in foraging modes. Early winter foraging is presumably distinct from the late-winter foraging pattern that focuses almost entirely on arboreal lichen from standing trees, described above.

Foraging patterns, particularly feeding intensity and distance between feeding sites, might be influenced by group size, so absolute values reported here may have been related to the small groups we trailed. In addition, differences in sampling methods make detailed comparisons among studies difficult. In spite of those issues, some comparisons can be made to early-winter patterns recorded at similar scales elsewhere in Mountain Caribou range. The larger diameter of trees on sites or transects where Caribou fed relative to where they did not feed was also reported by McLellan and Flaa (1993*) but not by Mowat et al. (1998*), and below but not within subalpine forest by Ashcroft (1997*). The greater arboreal lichen abundance on used trees was also found elsewhere (Mowat et al. 1998*; Terry et al. 2000). Differences in tree species composition between used sites and unused or random sites have not been reported outside of the Purcell Mountains (McLellan and Flaa 1993*; Mowat et al. 1998*; Terry et al. 2000). Similar to our results, Terry et al. (2000) did not find live:dead tree ratios to differ relative to Caribou use, but Ashcroft (1997*) noted greater Caribou use with increasing proportions of live trees in some habitat types. Although we have made incidental observations of Caribou using Falsebox and forbs in early winter within this study area in other years, they were not recorded during this study. Falsebox use has been reported within some populations (McLellan and Flaa 1993*; Mowat et al. 1998*), but not others (Ashcroft 1997*). We are not aware of any other records of Grouseberry use within the range of this ecotype. Another major contrast between our results and those reported elsewhere was that we observed no use of habitats below the subalpine forest (although that is not always true for this study area; T. Kinley, unpublished data). The contrasts with other populations probably relate both to permanent environmental factors related to our study area's location on the somewhat drier southeastern edge of Mountain Caribou range and to conditions in the year of the study, in which snow accumulated rapidly. However, the emphasis on downed trees and branches or litterfall

during early winter is consistent with the findings of Simpson et al. (1987), Rominger and Oldemeyer (1989), McLellan and Flaa (1993*), Ashcroft (1997*), Mowat et al. (1998*), and Terry et al. (2000), and is predictable given the greater lichen availability when trees are horizontal than when they are vertical. Rominger et al. (2000) found that Caribou could not maintain adequate forage intake in early winter without the presence of windthrown trees. During early winter, it becomes increasingly difficult to obtain ground-based foods as snowpacks deepen, yet lift is not yet adequate to reach the zone of abundant arboreal lichen high in trees, so arboreal lichen from sources other than standing trees may be essential. The apparent decline in the use of arboreal lichen fragments on the snow or on downed trees and branches during late winter likely relates not only to the increasing availability of lichen on standing trees, but also to a decreasing availability of downed arboreal lichen in late winter. A decrease in downed sources of arboreal lichen would be expected during late winter due to more stable weather (fewer storms with accompanying winds), frozen ground (less chance of roots breaking free of the soil), and attrition of the weaker trees, branches or lichen fragments by that point.

Patterns of tree selection at the foraging-path scale differed slightly from those noted for coarser spatial scales in the same study area. Apps and Kinley (2000*) found that, at a range of "landscape-level" scales, Caribou selected forests that contained Subalpine Fir, Whitebark Pine and Alpine Larch, showed nil to slightly positive selection for Engelmann Spruce, and nil to negative selection for Lodgepole Pine in early winter. At a scale that compared used to random sites 300 to 900 m apart, Kinley and Apps (2000*) similarly found a preference for Alpine Larch and Whitebark Pine, but no selection relative to Engelmann Spruce, Subalpine Fir or Lodgepole Pine. In contrast, results presented here indicate a preference for Engelmann Spruce and Subalpine Fir relative to Alpine Larch, Whitebark Pine and Lodgepole Pine (Table 3). Differences among spatial scales in habitat selection by Woodland Caribou have been reported elsewhere (Rettie and Messier 2000; Apps et al. 2001). In addition to potentially being artifacts of among-scale differences in the definitions or physical configuration of "available" habitat, these differences may reflect hierarchical reactions by Caribou to limiting factors. Coarser-scale selection may relate to avoiding factors that are most limiting, such as predation, with finer-scale choices being related to factors that have a less catastrophic impact, such as food availability (Rettie and Messier 2000). In our study area, arboreal hair lichen, Grouseberry and terrestrial lichen are available to varying degrees across a broad range of elevations. However, lower elevations are used in winter by Moose (*Alces alces*), Elk (*Cervus elaphus*), Mule Deer (*Odocoileus hemionus*), and White-tailed Deer (*Odocoileus virginianus*) (Edwards 1956; Hudson et al. 1976) and therefore the Cougars (*Felis concolor*) and Gray Wolves (*Canis lupus*) that feed upon them. Predation has been a major limiting factor in several Mountain Caribou populations (Seip 1992; Kinley and Apps 2001). Caribou in the southern Purcell Mountains are likely influenced by a higher-level need to minimize predation risk by remaining at upper elevations; i.e., forests with a high Alpine Larch and Whitebark Pine component at the subalpine forest – subalpine parkland ecotone. In such locations, Gray Wolves and Cougars are nearly absent in winter, and lines of sight are aided by the open forest and little understory extending above the snowpack, improving the ability to avoid Wolverines (*Gulo gulo*), the only predator remaining at high elevations during winter. At the opposite end of the habitat-selection spectrum, Caribou make finer-scale decisions along foraging paths that relate to maximizing feeding opportunities, such as selecting tree species that provide a better substrate for lichen growth. Subalpine Fir and Engelmann Spruce have many low branches and evergreen needles to support lichen within reach of Caribou, whereas older trees of both pine species and Alpine Larch are typically devoid of live lower branches and Alpine Larch sheds its needles prior to winter. Thus, our results should be considered within a hierarchical framework of habitat selection.

Management Implications

Maintaining early-winter forage for Mountain Caribou in the southern Purcell Mountains will involve retaining the old forest stands that have abundant Grouseberry and arboreal lichen and significant rates of windthrow among lichen-bearing trees. Despite early-winter habitat typically being in the upper subalpine forest or the subalpine parkland, where overall timber values are presumably lower, Caribou select large individual Subalpine Fir and Engelmann Spruce trees, which can be economically valuable, and were recorded at the lower limit of the subalpine forest. Thus, when applying broader-scale models to determine areas where timber harvesting is to be excluded or modified for the benefit of Mountain Caribou (Stevenson et al. 2001), field-based inspections will also be essential to ensure that the reserves or management areas selected include characteristics suitable for early-winter foraging. They must also span a broad range of elevations. Given the greater movement between feeding sites observed during the ground-foraging period, relatively large areas of subalpine forests and parkland should be designated for management as early-winter habitat. Determining the temporal extent of ground-based foraging and the elevational range of both early-winter foraging modes in years of more typical snow accumulation, and determining the energetic costs associated with early winter, would clarify the relative importance of this period. This would aid future habitat management and protection decisions.

Acknowledgments

Funding for this research was provided by Resources Inventory Program grants from Forest Renewal British Columbia to the East Kootenay Environmental Society and Tembec Industries Inc., as part of the Purcell Caribou Project. We thank A. Levesque, M. Belcher, M. Panian, P. Cowtan and K. Eichenberger for arranging funding and administering the project; B. McLellan and J. Flaa for advice on sampling procedures; K. Hebert and L. Earl for aerial telemetry; and D. Heard and an anonymous reviewer for thorough and helpful reviews of an earlier draft.

Documents Cited [marked * in text]

Apps, C. D., and **T. A. Kinley.** 2000. Multi-scale habitat associations of mountain caribou in the southern Purcell Mountains, British Columbia. Prepared for East Kootenay Environmental Society, Kimberley, British Columbia, and Tembec Industries Inc., Cranbrook, British Columbia. 34 pages.

Ashcroft, G. 1997. Mountain caribou behaviour and microhabitat characteristics in the Quesnel Highland. Prepared for Ministry of Environment, Lands and Parks, Williams Lake, British Columbia. 30 pages.

Committee on the Status of Endangered Wildlife in Canada. 2002. Canadian species at risk, May 2002. Canadian Wildlife Service, Environment Canada, Ottawa, Ontario. 39 pages.

Conservation Data Centre. 2003. *Rangifer tarandus* pop. 1. http://srmwww.gov.bc.ca/cdc/tracking.htm. Viewed November 2003.

Hatter, I., D. Butler, A. Fontana, D. Hebert, T. Kinley, S. McNay, B. Nyberg, D. Seip, J. Surgenor, M. Tanner, L. Williams, G. Woods, J. Woods, and **J. Young.** 2002. A strategy for the recovery of mountain caribou in British Columbia. Version 1.0. Ministry of Water, Land and Air Protection, Victoria, British Columbia. 73 pages.

Kinley, T. A., and **C. D. Apps.** 2000. Selection for stand-level forest attributes by mountain caribou in the southern Purcell Mountains, British Columbia. Prepared for East Kootenay Environmental Society, Kimberley, British Columbia, and Tembec Industries Inc., Cranbrook, British Columbia. 19 pages.

McLellan, B. N., and **J. Flaa.** 1993. Integrating mountain caribou and forestry – the Revelstoke caribou project. E.P. 1161. Annual report year one. Ministry of Forests, Revelstoke, British Columbia. 34 pages.

Mowat, G., T. Kinley, and **S. Pendray.** 1998. Caribou site level habitat selection and home range patterns in the North Thompson watershed of British Columbia. Prepared for Ministry of Environment, Lands and Parks, Kamloops, British Columbia. 46 pages.

United States Fish and Wildlife Service. 1994. Recovery plan for woodland caribou in the Selkirk Mountains. United States Department of the Interior, Portland, Oregon. 71 pages.

Literature Cited

Antifeau, T. D. 1987. The significance of snow and arboreal lichen in the winter ecology of mountain caribou (*Rangifer tarandus caribou*) in the North Thompson watershed of British Columbia. MSc thesis, University of British Columbia, Vancouver, British Columbia. 142 pages.

Apps, C. D., B. N. McLellan, T. A. Kinley, and **J. P. Flaa.** 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. Journal of Wildlife Management 65: 65-77.

Armleder, H. M., S. K. Stevenson, and **S. D. Walker.** 1992. Estimating the abundance of arboreal forage lichens. Land Management Handbook Field Guide Insert 7, Ministry of Forests, Victoria, British Columbia. 22 pages.

Bloomfield, M. I. 1979. The ecology and status of mountain caribou and caribou range in central British Columbia. MSc thesis, University of Alberta, Edmonton, Alberta. 318 pages.

Curran, M. P., T. F. Braumandl, and **D. L. DeLong.** 1992. Climatic regions and biogeoclimatic zones of the Nelson Forest Region. Pages 29-43 *in* A field guide for site identification for the Nelson Forest Region. *Compiled and edited by* T. F. Braumandl and M. P. Curran. Land Management Handbook 20, Ministry of Forests, Victoria, British Columbia. 311 pages.

Edmonds, E. J. 1991. Status of woodland caribou in western North America. Rangifer Special Issue 7: 91-107.

Edwards, R. Y. 1956. Snow depths and ungulate abundance in the mountains of western Canada. Journal of Wildlife Management 20: 150-168.

Edwards, R. Y., and **R. W. Ritcey.** 1960. Foods of caribou in Wells Gray Park, British Columbia. Canadian Field-Naturalist 74: 3-7.

Edwards, R. Y., J. Soos, and **R. W. Ritcey.** 1960. Quantitative observations on epidendric lichens used as food by caribou. Ecology 41: 425:431.

Freddy, D. J. 1974. Status and management of the Selkirk caribou herd, 1973. MSc thesis, University of Idaho, Moscow, Idaho. 132 pages.

Goward, T. 1998. Observations on the ecology of the lichen genus *Bryoria* in high elevation conifer forests. Canadian Field-Naturalist 112: 496-501.

Heard, D. C., and **K. L. Vagt.** 1998. Caribou in British Columbia: a 1996 status report. Rangifer Special Issue 10: 117-123.

Hudson, R. J., D. M. Hebert, and **V. C. Brink.** 1976. Occupational patterns of wildlife on a major East Kootenay winter-spring range. Journal of Range Management 29: 38-43.

Kinley, T. A., and **C. D. Apps.** 2001. Mortality patterns in a subpopulation of endangered mountain caribou. Wildlife Society Bulletin 29: 158-164.

Rettie, W. J., and **F. Messier.** 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23: 466-478.

Rominger, E. M., and **J. L. Oldemeyer.** 1989. Early-winter habitat of woodland caribou, Selkirk Mountains, British Columbia. Journal of Wildlife Management 53: 238-243.

Rominger, E. M., and **J. L. Oldemeyer.** 1990. Early-winter diet of woodland caribou in relation to snow accumulation, Selkirk Mountains, British Columbia, Canada. Canadian Journal of Zoology 68: 2691-2694.

Rominger, E. M., C. T. Robbins, M. A. Evans, and **D. J. Pierce.** 2000. Autumn foraging dynamics of woodland caribou in experimentally manipulated habitats, northeastern Washington, USA. Journal of Wildlife Management 64: 160-167.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology 70: 1494-1503.

Simpson, K., K. Hebert, and **G. P. Woods.** 1987. Critical habitats of caribou (*Rangifer tarandus caribou*) in the mountains of southern British Columbia. Wildlife Working Report WR-23, Ministry of Environment and Parks, Victoria, British Columbia. 12 pages.

Stevenson, S. K., H. M. Armleder, M. J. Jull, D. G. King, B. N. McLellan, and **D. S. Coxson.** 2001. Mountain caribou in managed forests: recommendations for managers. Second edition. Wildlife Report R-26, Ministry of Environment, Lands and Parks, Victoria, British Columbia. 76 pages.

Stevenson, S. K., and **D. F. Hatler.** 1985. Woodland caribou and their habitat in southern and central British Columbia. Volume 1. Land Management Report 23, Ministry of Forests, Victoria, British Columbia. 355 pages.

Terry, E. L., B. N. McLellan, and **G. S. Watts.** 2000. Winter habitat ecology of mountain caribou in relation to forest management. Journal of Applied Ecology 37: 589-602.

Received 26 February 2001
Accepted 15 December 2003

A Review of the Canada Lynx, *Lynx canadensis*, in Canada*

KIM G. POOLE

Aurora Wildlife Research, 2305 Annable Rd., Nelson, British Columbia V1L 6K4 Canada

Poole, Kim G. 2003. A review of the Canada Lynx, *Lynx canadensis,* in Canada. Canadian Field-Naturalist 117(3): 360-376.

The Canada Lynx (*Lynx canadensis*) is the most common and widespread member of the cat family in Canada. Lynx are distributed throughout forested regions of Canada and Alaska and into portions of the northern contiguous United States, closely paralleling the range of its primary prey, the Snowshoe Hare (*Lepus americanus*). They are most common in the boreal, sub-boreal and western montane forests, preferring older regenerating forests (>20 years) and generally avoiding younger stands, and occupy roughly 95% of their former range in Canada. Lynx population size fluctuates 3–17 fold over an 8–11 year cycle, tracking the abundance of Snowshoe Hares with a 1–2 year lag. During increasing and high hare abundance, lynx have high reproductive output and high kit and adult survival. The decline phase is characterized by reproductive failure, increased natural mortality, and high rates of dispersal. Dispersal distances of over 1000 km have been recorded. During the cyclic low, kit recruitment essentially fails for 2–3 years, and is followed by several years of modest reproductive output. Reproductive parameters in southern lynx populations appear similar to those found during the cyclic low and early increase phase in more northern populations. Trapping is a significant source of mortality in some areas. Field studies have documented from 2–45 lynx/100 km^2 at various times in the cycle and in various habitats. Although the amplitude of the cyclic fluctuations in lynx numbers may have decreased somewhat in recent decades, there is no evidence to suggest a significant decline in numbers in Canada. Lynx are managed as a furbearer in Canada, with harvest regulated primarily by seasons, quotas, and closures. The harvest over the past decade has declined concurrent with declining pelt prices, and is currently a fraction of historic levels. Lynx are fully protected in less than 2–3% of their range in Canada. There is no evidence to suggest that overall lynx numbers or distribution across Canada have declined significantly over the past two decades, although loss of habitat through increased urbanization and development and forestry is likely affecting lynx populations along the southern fringe of its range. Its high potential to increase in numbers and propensity to disperse long distances suggest that the species is relatively resilient to localized perturbations and reductions, given time and removal of the factors that cause the initial decrease. Lowered lynx harvests, coupled with a greater awareness of the need for proactive lynx management, suggests that the overall future of lynx in Canada is secure.

Key Words: Canada Lynx, *Lynx canadensis*, COSEWIC, Canada, status, review, ecology.

The Canada Lynx (*Lynx canadensis*), the most common wild felid in Canada, is an elusive inhabitant of the forests across much of Canada. Its cyclic fluctuations in numbers, tied closely to those of the Snowshoe Hare (*Lepus americanus*), have long fascinated trappers and biologists alike. This report summarizes the ecology and current status and management of the Canada Lynx in Canadian jurisdictions. It is based on a report requested by the Terrestrial Mammals Specialist Group of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Poole 2001*), and updates information provided in the original COSEWIC status report by Stardom (1989*).

The Canada Lynx has been considered by some authors as conspecific with Eurasian Lynx *Lynx (Felis) lynx* (Linnaeus 1758) (Kurtén and Rausch 1959; McCord and Cardoza 1982; Quinn and Parker 1987; Tumlison 1987); however, large differences in size and marked adaptive differences in prey selection (Nowell and Jackson 1996) and mitochondrial DNA analysis of the *Lynx* taxa (Beltrán et al. 1996; O'Brien 1996) tend to support full species status for the Canada Lynx (Hall 1981; Wozencraft 1993). The taxonomy of the cat family is an area of much disagreement (Werdelin 1996), and further debate will surely occur.

Two subspecies have been recognized (Banfield 1974; Tumlison 1987), *L. c. canadensis* (Kerr 1792) from mainland northern United States and Canada, and *L. c. subsolanus* (Bangs 1897), a smaller brownish race restricted to the island of Newfoundland. However, van Zyll de Jong (1975) concluded that there was no support for treating the Newfoundland population as a distinct subspecies based on traditional morphological traits, suggesting that the species is monotypic in North

* This paper is condensed from the official COSEWIC status report submitted to COSEWIC by the author on which a Not at Risk status was assigned by COSEWIC in May 2001. For access to the official report, contact the Committee on the Status of Endangered Wildlife in Canada at the Canadian Wildlife Service, Ottawa, Canada, or the author.

America. The evolutionary history of the Canada Lynx is unclear. The Canada Lynx and Bobcat (*Lynx rufus*) probably resulted from separate invasions of the Eurasian Lynx across the Bering Land Bridge during interglacial periods of the Pleistocene; the first resulted in speciation to the more southern Bobcat, and the second invasion in speciation into the Canada Lynx (Werdelin 1981, 1983).

Description

The Canada Lynx (hereafter lynx) is a medium-sized cat with a flared facial ruff, black ear tufts, large padded feet, and a short, black-tipped tail (Banfield 1974; Quinn and Parker 1987). Their pelage is reddish to grey-brown, being lighter during winter; the hairs are generally tipped in light grey or white. A rare colour phase, the "blue lynx", has pallid, bluish grey fur that suggests partial albinism. Lynx show mild sexual dimorphism in size, males (averaging 80–90 cm long and 9–14 kg) being 15–25% larger than females (76–84 cm long and 8–11 kg; Quinn and Parker 1987; K. Poole, unpubl. data). Their long hair, especially during winter, makes them appear much larger. Subtle differences in size of lynx occur across Canada with the largest individuals found in northern areas.

Distribution

The lynx has a wide distribution covering most of northern North America, with the species currently occupying roughly 95% of its former Canadian range, approximately 5 500 000 km^2 (Figure 1). In contrast to the Canadian distribution, lynx distribution in the northern contiguous United States has been greatly reduced and fragmented, largely as a result of human-induced mortality, human settlement and likely habitat alteration during the past 2 centuries (McKelvey et al. 2000). Due to cyclic pulses of dispersal, lynx occasionally occur to varying degrees in areas peripheral to its primary range.

The northern extent of lynx distribution in Canada appears to have changed little compared to historic distribution (Figure 1). Treeline defines the northern boundary throughout Alaska, Yukon, Northwest Territories, Nunavut, Québec and Labrador. Lynx are absent or uncommon in the wet coastal forests of the west coast. Lynx are absent from the southern third of the Prairie Provinces where their southern limit has likely been pushed slightly northward because of conversion of land to agriculture. Lynx were extirpated from Prince Edward Island during the latter half of the 1800s and mainland Nova Scotia in the early 1950s, and occur

FIGURE 1. Historic (dotted lines) and 2001 (shaded areas) distribution of the Canada Lynx in North America. Historic distribution in Canada from de Vos and Matel (1952) and van Zyll de Jong (1971) (see text). Current Canadian distribution from jurisdiction biologists, and Alaska distribution from H. Golden (personal communication). Historic and current distribution in the contiguous United States from Maj and Garton (1994) and McKelvey et al. (2000).

in very low numbers throughout New Brunswick, with their greatest numbers in the northwest corner of the province. Their range on Cape Breton Island, Nova Scotia, has been reduced to highland habitat. Settlement and conversion of forest to farmland has eliminated lynx from much of the once extensive mixed deciduous and coniferous forests of the southern half of southern Ontario and portions of Québec in the Eastern Townships bordering the New England states. The map in de Vos and Matel (1952) as redrawn from Seton (1929) may not have accurately depicted the historic southern boundary of lynx distribution because large portions of the Prairie ecoregion were included (Bailey 1998); this was likely poor lynx habitat even in historic times. Extensive surveys by Maj and Garton (1994) and McKelvey et al. (2000) do not support this historic distribution in the Prairie biome in the contiguous United States.

Most lynx populations cycle dramatically on an 8–11 year basis (see General Biology, below). Some areas within the normal distribution of the species may become devoid of lynx for several years during population lows. Lynx often undertake large dispersal movements, primarily in response to region-wide cyclic reductions in Snowshoe Hare populations (see Movements, below). These pulses of dispersal, with some individuals moving >500 km (Ward and Krebs 1985; Slough and Mowat 1996; O'Donoghue et al. 1997; Poole 1997), result in periodic shifts of distribution into the periphery of areas where they do not normally occur (Banfield 1974; Mech 1973, 1977). These populations may persist for only a few years or, given the right circumstances, may establish breeding populations. The cyclic fluctuations in density and dispersal patterns result in a distribution pattern that is difficult to accurately depict.

Habitat

Lynx occupy the boreal, sub-boreal and western montane forests of North America (McCord and Cardoza 1982; Quinn and Parker 1987). Although they occur in many forest types that are not truly boreal, lynx reach their highest densities in boreal and mixedwood forests dominated by spruce (*Picea* spp.), pine (*Pinus* spp.) and Balsam Fir (*Abies balsamifera*) with a variable deciduous component (Legendre et al. 1978; Quinn and Thompson 1987; Hatler 1988; Dwyer et al. 1989; Mowat et al. 2000). Lynx also occur in subarctic forests dominated by Balsam Fir and Paper Birch (*Betula papyrifera*) (Legendre et al. 1978). In the Maritimes and New England states, lynx are found in Balsam Fir and Black Spruce (*Picea mariana*) forests, and are often associated with spruce bogs (Parker 1981; Litvaitis et al. 1991; Aubry et al. 2000). In parts of western Canada (i.e., central and northern Alberta) lynx occur in upland aspen (*Populus tremuloides*) forests. In the western mountains, they occur in a more patchy distribution predominantly within the subalpine forest zone at elevations of 1200 to 3000 m, in spruce-Subalpine Fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*) and fir-hemlock (*Tsuga* spp.) forests (Koehler and Aubry 1994; Aubry et al. 2000). Lodgepole Pine (*Pinus contorta*) is found in these montane forests as a seral species on drier sites.

Stand level preferences by lynx follow closely those of its main prey, the Snowshoe Hare (Hodges 2000a, 2000b; Mowat et al. 2000). Lynx prefer older regenerating forest stands, greater than about 20 years of age, and generally avoid younger stands (Parker 1981; Kesterson 1988; Thompson 1988; Major 1989; Thompson et al. 1989; Perham 1995; Staples 1995; Mowat and Slough 2003). Many authors have demonstrated use (though not selection) of mature forest stands, especially those included within burns (Kesterson 1988; Staples 1995; Poole et al. 1996). The use of habitat edges (Kesterson 1988; Major 1989; Staples 1995) may be an important hunting strategy for lynx, which may allow them to hunt hares that live in habitats that are normally too dense to hunt effectively (Mowat et al. 2000). Although lynx select against use of openings such as meadows, farmland, and water bodies, they occasionally cross them (Murray et al. 1994; Fortin and Huot 1995; Poole et al. 1996; Mowat et al. 2000).

Lynx den sites described in the literature have similar structural attributes regardless of stand type or age. Denning habitat ranges from regenerating to mature stands, but most sites are associated with relatively dense vegetation in a tangle of wind-felled trees and deadfall or roots providing some form of overhead protection (Berrie 1974; Stephenson 1986*; Kesterson 1988; Koehler 1990; Slough 1999).

Wildfire, which is the most important factor in the dynamics of the northern boreal forest ecosystem (Kelsall et al. 1977; Viereck 1983), is a major habitat modifier (Johnson et al. 1995; Paragi et al. 1997). Logging, which is also an important factor in the dynamics of many boreal and montane forests, restarts the succession necessary to create optimum hare and lynx habitat, but often removes the structure needed for denning by lynx and the dense understory resulting from wildfire (Mowat and Slough 2003). Suppression of wildfire has likely reduced lynx habitat quality in some areas, especially in the south, by reducing the amount of early successional stands (Mowat and Slough 2003); however, at the landscape level the degree of impact is unknown. However, vast areas of Canadian forest burn each year despite suppression efforts. In western montane and southern landscapes, lynx habitat is fragmented by low elevation valleys and interspersions of unsuitable habitat (i.e., urban areas, transportation corridors, and agricultural lands). Habitat loss coupled with intensive settlement is probably the major cause of reduced lynx range in southern Ontario and Québec.

General Biology

The biology of the lynx is closely tied to the biology of the Snowshoe Hare. Lynx numbers fluctuate in synchrony over vast areas in response to population levels of hares; the decline in lynx numbers generally lags 1–2 years behind the decline in hare numbers (Elton and Nicholson 1942; Butler 1953; Keith 1963; Brand and Keith 1979; Boutin et al. 1995). Lynx densities in most central and northern populations change 3 to 17-fold during a cyclic fluctuation (Keith et al. 1977; Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 1997). In the southern boreal and montane forests Snowshoe Hare populations fluctuate, but at much lower amplitudes (Hodges 2000b). Southern lynx populations are not believed to exhibit cyclic fluctuations in density (Koehler and Aubry 1994); however, other than trapping records, which can be influenced by lynx dispersal from great distances and trapper effort, little objective data are available (Koehler 1990; Aubry et al. 2000). During the 1900s, lynx cycles appear to initiate and emanate from central Canada, following similar trends in the hare cycle (Smith 1983; Hodges 2000a), such that peak lynx harvests in Saskatchewan and Manitoba from 1960 to 1980 occurred around the turn of the decade, and 2–4 years later in Yukon, Alaska, and Québec.

The cycle in lynx numbers is often broken into phases (Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 1997). The low period typically lasts 3–5 years and is denoted by low population density and a mild decline and recovery in numbers through the period. During the increase phase, about 3 years in duration, lynx numbers increase quickly, a result of high fecundity, high kit survival, and low adult mortality. The peak phase is usually a 2-year period of high lynx density with modest or no population growth. The decline or crash phase of the hare cycle is 1–2 years in duration; after a 1–2-year lag in timing, lynx numbers also decline dramatically during this phase of the cycle due to increased dispersal, high natural mortality, and a collapse in recruitment.

Reproduction

When hares are abundant, lynx have high reproductive potential; adult fecundity is high, litter size averages 4–5, kitten survival is high, and yearling lynx reproduce. During the cyclic low, recruitment essentially fails for about two years, and is followed by several years of modest recovery. Reproductive parameters in southern lynx populations appear similar to those observed during the later part of the cyclic low in more northern populations (Aubry et al. 2000).

Lynx breed through March into early April (Quinn and Parker 1987) and breeding pairs may remain together for several days (Poole 1994; Mowat and Slough 1998). During periods of high hare density essentially all adult female lynx ovulate each year, but this proportion declines during periods of hare scarcity (O'Connor 1984; Quinn and Thompson 1987). Gestation is approximately 60–65 days (Quinn and Parker 1987; Koehler and Aubry 1994). Most births occur in the later third of May and into early June (Mowat et al. 1996b; Slough and Mowat 1996; K. Poole, unpubl. data). Den sites are usually surface scrapes (Mowat 1993; Slough 1999).

Yearling females reproduce when hares are abundant (Brand and Keith 1979; Quinn and Thompson 1987; Slough and Mowat 1996); parturition by yearling lynx may be delayed approximately 2–3 weeks compared to adults (Mowat et al. 1996b; Slough and Mowat 1996). Few if any yearlings conceive during periods of low hare density (Parker et al. 1983). Male lynx are thought to be incapable of breeding in their first year (McCord and Cardoza 1982; Quinn and Parker 1987). Breeding may continue into old age; the oldest lynx recorded in the wild were 13–14 years of age (Quinn and Thompson 1987; Chubbs and Phillips 1993).

Placental scar counts suggest that at high hare densities pregnancy rates of lynx range from 73–93% for adults and 33–100% for yearlings (Brand and Keith 1979; Parker et al. 1983; O'Connor 1984; Quinn and Thompson 1987; Slough and Mowat 1996). Field observations suggest that birth rates range from 73 to 100% for adults and 33 to 100% for yearlings during this period (Poole 1994; Mowat et al. 1996b; and see Table 3 in Mowat et al. 1996a:438). During the increase and peak phase of the hare cycle, litters produced by adult females average 4–5 kittens, and juvenile survival is high (50–83%) (Brand et al. 1976; Poole 1994; Mowat et al. 1996a; Slough and Mowat 1996). Yearling lynx may contribute little to recruitment; even in high quality habitat when hares peaked in south-central Yukon survival of kittens of yearling mothers was low (<26%; Mowat et al. 1996b; Slough and Mowat 1996). In southern populations few kittens are born or survive until winter and litter size is small; in north-central Washington only four litters averaging two kittens each were observed among 12 resident females over four winters (Brittell et al. 1989). Similarly low birth rates and litter sizes have been recorded in other southern lynx populations, although sample sizes are small (Aubry et al. 2000).

Adult and yearling lynx birth rate is reduced the spring following the hare decline (Poole 1994; Slough and Mowat 1996). Kitten survival also declines to near zero the year after (Brand et al. 1976; Parker et al. 1983; Poole 1994) or two years after (Slough and Mowat 1996) hare numbers crash. Adult females continue to conceive during the cyclic hare low in northern lynx populations, but live births are few or none, a result of lower reproductive rates, preimplantation and intrauterine losses, and neonatal mortality (Nellis et al. 1972; Parker et al. 1983; O'Connor 1984; Poole 1994; Slough and Mowat 1996). No studies have reported kittens present during the second winter following the hare crash (Brand et al. 1976; Poole 1994;

Slough and Mowat 1996; O'Donoghue et al. 1997). However, there are anecdotal reports of kittens present throughout the cycle in the north in pockets of optimum hare and lynx habitat (Mowat et al. 2000). Recruitment essentially fails for 3–4 years (Brand and Keith 1979; Parker et al. 1983; Poole 1994; Mowat et al. 1996b), but female lynx may begin to give birth before an appreciable recovery in hare numbers, as shown by observations of live litters or kittens in carcass collections conducted prior to the hare increase (Brand et al. 1976; Slough and Mowat 1996). Thus, northern lynx populations do recruit some individuals when hares are scarce and these individuals may be important in maintaining lynx populations through a hare low phase (Mowat et al. 2000). As hare numbers increase, yearling females begin to breed and adult litter size increases (Brand and Keith 1979; O'Connor 1984; Slough and Mowat 1996).

Survival

Survival of lynx varies greatly as Snowshoe Hare abundance changes throughout the cycle in northern populations, and is influenced by the level of trapping in and around the population under study. In the Yukon and NWT, annual survival rates of adults during the increase and peak phase of the hare cycle were >0.70 in a lightly trapped population and >0.89 in largely untrapped populations (Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 1997). Annual survival rates of adult lynx remained high (0.78–0.95; Poole 1994; Slough and Mowat 1996) or declined moderately (0.45–0.63; O'Donoghue et al. 1997) through the 1 or 2-year hare decline. The first year of very low hare numbers was characterized by low adult survival (0.09–0.40), followed by higher survival in the subsequent 1–2 years of low hare densities (0.63–0.82; Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 1997). Survival rates in areas of high trapping pressure are generally lower; on the Kenai Peninsula in Alaska, Bailey et al. (1986) found that trapping removed 80% of individuals over one year. Kitten survival was high (50–83%) during the increase and peak phase of the hare cycle but declined to near zero 1–2 years after hare numbers crashed (Brand et al. 1976; Parker et al. 1983; Poole 1994; Slough and Mowat 1996). In southern lynx populations, kitten survival rates appear to be low (0.12; Koehler 1990), but data are limited.

Survival tends to be lowest in winter; most mortality during low hare abundance occurred during mid-December to mid-February, and most natural mortality (primarily starvation) appears to coincide with <-35°C temperatures, when metabolic requirements increase (Poole 1994; O'Donoghue et al. 1995).

Earlier studies showed high trap-related mortality and essentially no natural mortality in lynx populations (Brand et al. 1976; Ward and Krebs 1985). Recent studies suggest a higher incidence of natural mortality: All adult deaths recorded in Washington were from natural causes (Brittell et al. 1989; Koehler 1990). In southwestern Northwest Territories the annual death rate from trapping (0.08) was higher than from natural causes (0.02) during peak and declining hare numbers; however, during low hare numbers the death rate was far higher from natural causes (primarily starvation; 0.48) than from trapping (0.20) (Poole 1994). All detected mortality of resident lynx was from natural causes during the first full year of low hare densities in south-central Yukon, although 20 marked lynx (27% of all emigrants) were trapped after dispersal (Slough and Mowat 1996). These results suggest that during the first two winters of hare scarcity, trapping mortality may be primarily compensatory to natural mortality, at least in lightly trapped areas.

Causes of natural mortality of lynx are difficult to determine; a radiocollar and tufts of hair provide little basis for inference. Ideally, mortality factors should also be identified as proximate or ultimate causes. Starvation (and related conditions) and cases of cannibalism have been recorded, primarily during low prey abundance (Poole 1994; O'Donoghue et al. 1995; Slough and Mowat 1996). Predation on lynx by Wolverine (*Gulo gulo*), Wolf (*Canis lupus*) and Coyote (*C. latrans*) has also been confirmed (Slough and Mowat 1996; O'Donoghue et al. 1995, 1997; Buskirk et al. 2000). Lynx harbour a diverse parasite fauna, including nematodes, cestodes, trematodes, lice and fleas (van Zyll de Jong 1966a; McCord and Cardoza 1982; Smith et al. 1986; Quinn and Parker 1987), but their influence on lynx health and survival is unknown.

Movements

Recent studies have documented numerous examples of long distance (>100 km) movements (Ward and Krebs 1985; Brittell et al. 1989; Perham et al. 1993; O'Donoghue et al. 1995, 1997; Slough and Mowat 1996; Poole 1997). Straight-line dispersal distances range up to 1100 km, with 15 documented cases from northern Canada of dispersal >500 km (Ward and Krebs 1985; Slough and Mowat 1996; O'Donoghue et al. 1997; Poole 1997). Three dispersals of 100–616 km have been documented from southern populations, all in a northward direction (Mech 1977; Brainerd 1985; Brittell et al. 1989). Dispersing lynx have crossed roads, multilane highways, and large rivers and lakes, sometimes during the snow-free season (Aubry et al. 2000; Mowat et al. 2000). Steep terrain and multilane highways may affect dispersal movements (Apps 2000). Note that all reported dispersal rates and distances must be considered potentially biased. Trappers supply most information on long-distance movements by lynx. Trapping returns are affected by the density and distribution of trapping around study areas, and by behavioural differences in trap vulnerability among age and sex classes of lynx (Bailey et al. 1986; Quinn and Thompson 1987; Slough and Mowat 1996; Poole 1997).

Emigration and immigration of lynx occurs throughout the hare cycle (Slough and Mowat 1996; O'Don-

oghue et al. 1997). Immigration rates balance or exceed losses to emigration during the rapid increase phase in lynx populations, while emigration rates increase and exceed immigration during the decline in hare abundance and the first full year of low hare densities (Slough and Mowat 1996). In southwestern NWT the annual probability of dispersal for adult lynx was low (<24%) at peak hare densities and during the hare decline, very high during the first 2 years of low hare numbers (78–100%), and then stabilized during the third and fourth years of low hare densities (<20%; Poole 1997). In southwestern Yukon, all long-distance dispersals of resident adults occurred during or at the end of the Snowshoe Hare decline (Ward and Krebs 1985; O'Donoghue et al. 1995).

Lynx dispersal may be characterized as either juveniles dispersing from natal areas ("innate dispersal"), or adults dispersing in response to an environmental "catastrophy" ("environmental dispersal"; Howard 1960) such as the hare decline faced by northern populations approximately every 10 years. Annual timing of dispersal varies. Juvenile lynx tend to disperse primarily in the spring, soon after independence. Most environmental dispersal occurs during the period of greatest nutritional stress, generally mid-winter to spring during or after a decline in hare density. The period of greatest dispersal in recent northern studies was March–June during the winter hare decline and during mid-winter of the subsequent 1–2 winters (O'Donoghue et al. 1995; Slough and Mowat 1996; Poole 1997). Dispersal rates or distances are generally greater for males than females of most mammalian species (Greenwood 1980; Wolff 1994); trapping returns are inherently biased towards males (Bailey et al. 1986; Quinn and Thompson 1987).

Initiation of dispersal in northern populations appeared to coincide with temperatures <-35°C (O'Donoghue et al. 1995; Poole 1997). Some dispersing lynx survived the hare crash and re-established home ranges some distance from their point of dispersal (verified at 65–85 km, potentially up to 1000 km; Slough and Mowat 1996; O'Donoghue et al. 1997; Poole 1997). These successful re-establishments are difficult to detect using conventional study methods, and are likely under-reported. In southern lynx populations, no cases of successful dispersal (defined as breeding at the new location) have been reported, although again sample sizes are small (Aubry et al. 2000).

Nutrition

Snowshoe Hares are the key component of the diet of lynx across North America, comprising from one-third to nearly all of prey items identified (for food habit summaries see Quinn and Parker 1987:686; Koehler and Aubry 1994:75; O'Donoghue et al. 1998b; Mowat et al. 2000). Estimated maximum kill rates were about 0.8 hares (Keith et al. 1977) to 1.6 hares per day (O'Donoghue et al. 1998b, 2001). Other common prey items include Red Squirrels (*Tamiasciurus hudsonicus*), mice and voles, flying squirrels (*Glaucomys* spp.), ground squirrels (*Spermophilus* spp.), Beaver (*Castor canadensis*), Muskrat (*Ondatra zibethica*), grouse and ptarmigan (Galliformes and *Lagopus* spp.), and occasionally other birds and mammals. Ungulates, primarily young-of-the-year, are eaten as carrion and occasionally killed, most often during winter and at cyclic low hare abundance (Saunders 1963a; Bergerud 1971; Parker et al. 1983; Stephenson et al. 1991; Apps 2000; K. Poole, unpubl. data). Predation by lynx on Red Fox (*Vulpes vulpes*) and other lynx also occurs, again mostly during periods of low hare densities (Stephenson et al. 1991; O'Donoghue et al. 1995). Caching of food by lynx is rare (O'Donoghue et al. 1998b).

In lynx populations reliant on highly cyclic Snowshoe Hare populations, the proportion of hares in the diet of lynx generally declines and use of alternative prey increases as hares become scarce (Brand et al. 1976; Parker 1981; Parker et al. 1983; Stephenson et al. 1991; O'Donoghue et al. 1998b; K. Poole, unpubl. data). Red Squirrels in particular appear to be an important alternative food source for lynx during periods of low hare abundance. Red Squirrels became increasingly important (20–44% biomass) at the lowest hare density compared to almost no use (0–4% biomass) during years of high hare densities in southwestern Yukon (O'Donoghue et al. 1998b). Similarly, during years of hare scarcity, use of carrion, Red Squirrel, Ruffed Grouse (*Bonasa umbellus*), and other birds increased in central Alberta (Brand et al. 1976). Lynx generally take fewer Snowshoe Hare and more alternative prey in summer than in winter (Quinn and Parker 1987; Koehler and Aubry 1994). Most studies suggest that hares contribute about 25% less to lynx diet during summer compared to winter (van Zyll de Jong 1966b; Parker et al. 1983; Fortin and Huot 1995; Staples 1995). In southern lynx populations that contend with consistently low densities of hare, Red Squirrels may form about one-third of the diet (Koehler 1990; Apps 2000), and use of ground squirrels has been observed (Aubry et al. 2000).

Where Coyote and lynx are sympatric and share a limited resource base, dietary overlap during winter has been shown to be high; however, there is no evidence of interspecific or exploitation competition (Murray and Boutin 1991; Fortin and Huot 1995; Murray et al. 1995; Staples 1995; O'Donoghue et al. 1997, 1998a, 2001). Parker et al. (1983) postulated that Bobcats may exhibit competitive exclusion over lynx on Cape Breton Island.

Behaviour

Lynx have a social organization similar to that of other North American felids, consisting of social intolerance and mutual avoidance (Seidensticker et al. 1973; Bailey 1974; Brittell et al. 1989). This land tenure system has been described as "intrasexual territori-

ality" (Powell 1979; Kesterson 1988), where resident individuals maintain exclusive territories within each sex and males often but not always have larger home ranges than females. Lynx are passively territorial, and use feces, sprayed urine, or anal secretions to mark home ranges and provide both spatial and temporal information that may reduce confrontations (Saunders 1963b; Mellen 1993; Staples 1995). Some sort of spacing mechanism may operate to keep same-sex animals separated in time and space, but little or no active avoidance or overt defence of areas between overlapping or adjacent pairs has been detected, suggesting that this spacing is upheld by relatively passive means (Poole 1995). Male and female home ranges overlap completely while within-sex overlap is usually modest or may be confined to pairs of possibly related individuals per study (e.g., Poole 1995). Home range exclusiveness may be a function of degree; some overlap may occur at the 90 or 95% home range contour level, but little may occur among the 50% contour core areas (Poole 1995). Conflict among individuals is rare in lynx, but aggressive intra-species encounters do occur, primarily during years of food shortage (Poole 1994, 1995; O'Donoghue et al. 1995; Mowat and Slough 1998).

Lynx home range sizes vary among areas, sexes, seasons, and cyclical phases, although different methods of data collection, sample sizes and analysis techniques make it difficult to compare home range sizes among studies. Dramatic variation in home range size has been reported for lynx across their North American range (8–738 km^2; summarized in Quinn and Parker 1987; Koehler and Aubry 1994; Aubry et al. 2000; Mowat et al. 2000). During high hare density in northern lynx populations, annual home ranges of males often cover 20–45 km^2, and female 13–21 km^2; these increase 2–10 fold during low hare densities. Relatively large home ranges appear to be characteristic of southern lynx populations, similar to those found in the North during periods of low hare abundance. Male home range sizes are usually larger than female ranges (Kesterson 1988; Koehler and Aubry 1994; Fortin and Huot 1995; Perham 1995; Slough and Mowat 1996; O'Donoghue et al. 2001), but not always (Ward and Krebs 1985; Poole 1994). Both sexes show strong range fidelity, often over many years (Poole 1995; O'Donoghue et al. 2001), but home range shifts and abandonment are also common (Parker et al. 1983; Brittell et al. 1989; Koehler 1990; Poole 1994; Perham 1995; Slough and Mowat 1996; O'Donoghue et al. 2001).

Lynx home range size changes little before the hare crash but increases dramatically after the crash in northern Canada (Brand et al. 1976; Ward and Krebs 1985; Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 2001). However, a linear relationship between lynx home range size and hare abundance has not been demonstrated (Brand et al. 1976; Slough and Mowat 1996), even when compared against hare abundance the previous year (to accommodate the 1-year lag in response; O'Donoghue et al. 1997; Mowat et al. 2000).

Lynx home ranges vary seasonally, although the observed seasonal differences are inconsistent (Aubry et al. 2000). Females with kittens have smaller ranges and males during the breeding season have larger ranges (Kesterson 1988; Mowat and Slough 1998). Kittens remain with the mother throughout the winter; family groups begin to break-up in early March (Saunders 1963b; Brand et al. 1976; Parker et al. 1983; Poole 1995; Mowat et al. 1996b). Natal dispersal begins in late April to early May; some juveniles disperse immediately, while others remain in the natal area for up to one year after their first winter (Kesterson 1988; Poole 1994, 1995; Mowat et al. 1996b; Slough and Mowat 1996).

There is evidence to suggest that female pair bonds, either mother-daughter or sibling pairs, persist in lynx, and provide for a social system based on matrilineal descent (reviewed in Mowat et al. 2000). Female kittens sometimes establish home ranges within those of their mothers (Kesterson 1988; Slough and Mowat 1996), and adult females may retain contact with their female offspring throughout their life (Carbyn and Patriquin 1983; Staples 1995; Mowat and Slough 1998). Observations of some female home ranges with large overlap, possibly signifying related individuals, have been reported (Poole 1995; O'Donoghue et al. 1997). The persistence of female kin bonds in lynx populations may reduce investment in territorial defence (Mowat et al. 2000). Territoriality may be relaxed among relatives so that populations with related individuals may attain higher density (Mowat et al. 2000).

Other than direct influence through trapping activities, humans may exert potentially negative influences on lynx by building residences and roads in and through lynx habitat, by altering and modifying existing habitats, and by direct disturbance through recreation or travel in areas inhabited by lynx. Although much of the data are anecdotal, evidence suggests that lynx can tolerate at least some human disturbance and even continued presence of humans, including moderate levels of road and snowmobile traffic (Staples 1995; Mowat et al. 2000). Lynx occur at moderate densities in areas with dispersed agricultural areas and reasonably dense rural human populations (Brand and Keith 1979; Fortin and Huot 1995), and are observed crossing and alongside roads and residential areas in both Yukon and NWT (Mowat et al. 2000). Although lynx will generally flee when closely approached, they appear to become bolder and less wary of people during periods of low prey abundance. They are relatively easy to attract and capture, having little fear of human scent. Lynx may tend to avoid areas with higher levels of disturbance or greater fragmentation of habitat from development, although this hypothesis has not been rigorously tested.

Population Size and Trends

An accurate estimate of lynx population size is impossible over large areas. However, considering the extent of lynx habitat in Canada (roughly 5 500 000 km^2), densities during the low of 2 lynx/100 km^2, and a safety factor of 50%, there may be roughly 50 000 lynx in Canada during the cyclic low and over 500 000 during some cyclic peaks. The few intensive radio telemetry studies conducted in North America provide the data for most density estimates. Considering that many of these studies were conducted over relatively short time frames, with small sample sizes within poorly bounded study areas, and often for reasons other than density estimation, even these density estimates must be considered imprecise. Regional estimates are generally conservative extrapolations from intensive radio telemetry studies within different broad biophysical areas. Relative changes in lynx populations may be indexed using a variety of methods, such as snow track counts for Snowshoe Hares and/or lynx (Poole 1994; Labonté et al. 1999*; K. Poole, unpublished data), tracking changes in kits in the harvest using pelt length measurement (Quinn and Gardner 1984; Slough 1996) or carcass collections (Slough and Mowat 1996), and trapper questionnaires (Slough et al. 1987).

Peak densities of 30–45 lynx/100 km^2 have been observed in regenerating stands in the north (Poole 1994; Slough and Mowat 1996), and 8–20/100 km^2 in mature forests in the north and more southern ranges (Parker et al. 1983; Banville 1986; Noiseux and Doucet 1987; Kesterson 1988; Fortin and Huot 1995; O'Donoghue et al. 1997). Population densities during the low in all populations are typically 2–3 lynx/100 km^2. The few published studies in southern boreal forests suggest relatively static lynx densities of 2–3/100 km^2 (Koehler 1990; Aubry et al. 2000), typical of northern populations during the low in the hare cycle.

Fur harvest returns have provided records of lynx harvests for two centuries, and show dramatic changes in the amplitude in the cycle (Figure 2). Harvest returns, however, do not directly represent real population change. Harvest returns are affected by the host of factors influencing trapper effort and success, including changes in socio-economic conditions, season length, quota and trap type restrictions, fur prices, subsidies, mode of transportation, and access. Fur prices likely affect harvest effort over the short term (Brand and Keith 1979), but it may not be valid to compare inflation-adjusted prices and harvests that occurred decades apart.

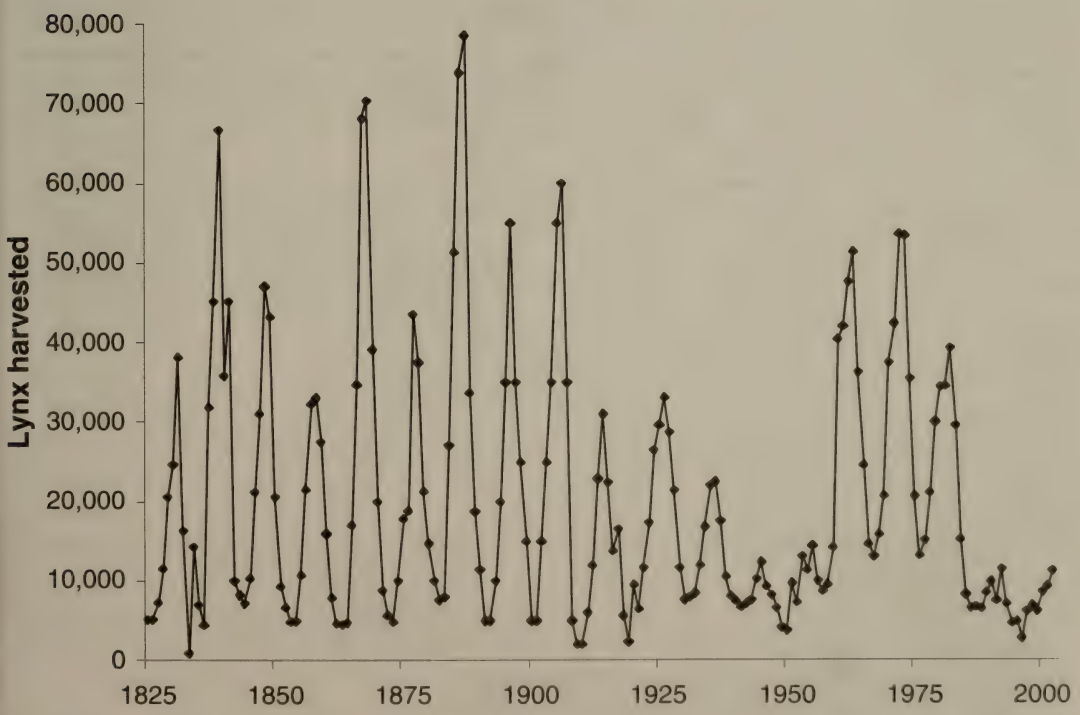


FIGURE 2. Canada Lynx harvest in Canada from 1825 to 2002, from Mowat et al. (2000:Figure 9.4) and Statistics Canada, updated to August 2003.

Citing declining harvest returns and anecdotal information, de Vos and Matel (1952) noted a decrease in lynx numbers and distribution in Canada between 1920 and 1950. They cited overtrapping and ecological changes in habitat, primarily as a result of forest harvesting, as the main factors responsible for the decrease. Several authors have suggested local populations also were overexploited during the cyclic low of the 1980s (Todd 1985; Bailey et al. 1986; Hatler 1988; Nowell and Jackson 1996). This period came after three cycles from 1960 to 1980 characterized by relatively high peak harvests, and, possibly more importantly, relatively high harvest levels during the cyclic lows (Figure 2). Peak harvests (summing the five-year harvest around each peak) from 1960 to 1980 were similar to peak harvests during the classic cycles of the late 1800s, but the five-year harvest during the lows of 1960 to 1980 were about 25% higher than the lows of the late 1800s. Snowmobiles became readily available in the late 1950s and early 1960s, likely influencing trapper access and coverage. Whether or not these increased harvest levels during the cyclic lows cumulatively had a significant impact on subsequent population levels is unknown. Harvest levels during the 1990 peak were about one quarter of peaks observed during the 1960s and 1970s, perhaps not unexpected given the 10-fold decrease in pelt prices over the last half of the 1980s, and hence lower trapper effort. In addition, subsequent to the late 1980s most Canadian jurisdictions enacted more restrictive trapping regulations in reaction to perceived overharvest, which also restricted harvest levels.

Provincial and territorial management agencies were questioned in late 1999 about the status and trend of lynx populations in their jurisdiction over the past two decades (Tables 1 and 2). Half of the 12 jurisdictions with lynx populations reported a stable population trend, one reported an unknown but likely stable trend, and three reported an unknown trend. On Cape Breton Island, Nova Scotia, a decreasing population trend and distribution was noted during the 1960s and 1970s concurrent with the invasion of Bobcats (Parker et al. 1983). Over the past two decades, lynx numbers in the highlands of the Island appear to have changed little, fluctuating with changes in the availability of Snowshoe Hare (G. Parker, personal communication). In Alberta, lynx numbers may be depressed in portions of their range, attributed to overharvest during the previous two decades (A. Todd, personal communication).

Despite the dramatic decrease in harvest through the 1990 cyclic peak, there is evidence that lynx populations in much of the northern range were cycling normally. The highest lynx densities recorded to date were obtained during the 1990–1992 peak in the southwest-

TABLE 1. Provincial and territorial Conservation Data Centre rankings[a] and jurisdiction status for Canada Lynx, as provided by agency biologists in fall 1999 and updated in 2003 from government websites.

Province/territory	Conservation Data Centre ranking[a]	Wild species 2000 general status[b]	Additional Provincial/territorial status
Newfoundland	Nfld island: S3S4 Labrador: S4	Secure	–
Prince Edward Island	Extirpated	Extirpated	–
Nova Scotia	S1	May be at risk	Red (species at-risk)
New Brunswick	S1	At risk	Regionally endangered (threatened with imminent extirpation)
Québec	S5	May be at risk	On list of species likely to be designated threatened or vulnerable
Ontario	S5	Secure	–
Manitoba	S5	Secure	–
Saskatchewan	S5	Sensitive	–
Alberta	–	Sensitive	–
British Columbia	S4	Secure	Yellow (species that are apparently secure and not at risk of extinction)
Yukon	–	Secure	–
Northwest Territories	–	Secure	–
Nunavut	–	Sensitive	–

[a] **S1**: Extremely rare throughout its range in the province. May be especially vulnerable to extirpation.
S2: Rare throughout its range in the province. May be vulnerable to extirpation due to rarity or other factors.
S3: Uncommon throughout its range in the province, or found in a restricted range, even if abundant in some locations.
S4: Frequent to common; apparently secure but may have a restricted distribution or there may be perceived future threats.
S5: Common to very common; demonstrably secure and essentially ineradicable under present conditions.

[b] Canadian Endangered Species Conservation Council (CESCC) 2001.
At risk: at risk of extirpation or extinction (i.e., endangered or threatened).
May be at risk: may be at risk of extirpation or extinction.
Sensitive: a species is not believed to be at risk of immediate extirpation or extinction but may require special attention or protection to prevent it from becoming at risk.
Secure: a species that is not at risk or sensitive.

ern Northwest Territories and southern Yukon (Poole 1994; Slough and Mowat 1996). Although the amplitude of lynx abundance may have decreased in some regions through the 1980s and 1990s, there is little evidence to conclude that harvest during the low of the 1980s had a long-term impact on contiguous northern lynx populations.

Temporal trends in the distribution and abundance of lynx are difficult to identify given the wide natural fluctuations in population size driven primarily by the 8–11 year Snowshoe Hare cycle and the difficulty in estimating population size. Areas occupied during the peak in lynx abundance may be abandoned during the cyclic low, only to be re-occupied in the subsequent increase. The amplitude of lynx abundance may be closely linked to the amplitude of peak densities of hares. No studies have monitored lynx densities over more than one complete cycle. However, hare densities may differ 2–3 fold among peaks (Hodges 2000b: Table 6.1) and lynx densities may also be expected to differ among peaks under natural situations. Anecdotal information based on community fur returns and local knowledge suggests that there has been no decrease in range detected in the Northwest Territories, Yukon, or Alaska through the 1980s and 1990s (K. Poole, B. Slough, H. Golden, unpublished data).

Over the past two decades lynx distribution may have been reduced along the southern edge of its range in Canada. Some areas may still be recovering from excessive harvest of the 1970s and 1980s, but these appear to be showing signs of recovery and are few in number. Over the vast majority of the country there is no evidence to suggest that lynx distribution or numbers have changed substantially.

Limiting Factors and Threats

Removal of lynx by trapping is a major cause of mortality in some lynx populations in Canada. Trapping may be primarily compensatory to natural mortality only during the dramatic decline in populations in lightly trapped areas (Poole 1994; Slough and Mowat 1996). Lynx are relatively easily trapped, and with extensive access and pressure, trapping can remove a large proportion of a population (Todd 1985; Bailey et al. 1986). On the other hand, lynx are relatively fecund and populations can increase rapidly during periods of increasing or abundant prey (Mowat et al. 1996b; Slough and Mowat 1996). Lynx also have been shown to disperse great distances, and therefore have the ability to re-colonize vacant habitats.

Incidental or illegal harvest of lynx may occur throughout its range, and have been raised as potential threats to Cape Breton Island animals, exacerbated by the increase in use of snares for sympatric species (M. Elderkin, personal communication; D. Banks, personal communication). No data are available on the extent of illegal harvest of lynx in Canada. In areas with short trapping seasons or quotas, the degree of incidental or illegal trapping may be substantial. However for most of Canada where relatively liberal trapping seasons and open quotas are the norm, incidental and illegal harvests are likely a very small proportion of the overall harvest.

Fire suppression in much of North America over the past century may have reduced the amount and quality of early to mid-successional hare and lynx habitat, and may place forests at risk of large, intensive burns that fail to mimic natural fire history (Mowat and Slough 2003). A trend in government is surfacing towards a "let it burn" policy in some areas, which may ultimately rebalance fire-driven succession in parts of the country. Logging restarts the succession necessary to create optimum hare and lynx habitat, but often removes the structure needed for denning by lynx. The logging, site preparation and silviculture techniques used for and after harvest influence the quality of lynx and hare habitat that results (Mowat and Slough 2003). Changes to forestry practices in recent years to provide habitats and structure post-logging more conducive to wildlife may reduce the impact of logging on lynx habitat.

While threats to habitat may affect lynx populations to varying degrees throughout its range, especially in more southern populations, the isolated Cape Breton Island lynx were the only animals identified in this review that may be negatively and directly influenced by threats to habitat. These perceived threats include habitat fragmentation and loss of mature softwood stands suitable for denning through forest pathogens, fire and forest harvesting (M. Elderkin, personal communication). As noted by Parker et al. (1983), large-scale forest harvesting operations, although initially reducing densities in specific areas, should ultimately benefit the population by producing productive mid-successional habitats.

Clearing of forested lands for agriculture and urban development should have a minor influence on lynx distribution since these primarily influence the southern fringe of lynx range in Canada. However, little data are available on changes in lynx distribution in more southern ranges in Canada. Development and human activity may render some habitat as unsuitable for lynx.

Interspecific competition, primarily with Bobcats and Coyotes, may influence the distribution and abundance of lynx, although direct evidence is lacking. The reduction in lynx distribution on Cape Breton Island occurred concurrent with the invasion of the island by Bobcats, and although a direct causal link has not been established, the circumstantial evidence for interspecific competition is compelling. Both Bobcats and Coyotes are poorly adapted to deep snow. Buskirk et al. (2000) suggested that man-made trails facilitate access by Coyotes and Bobcats into areas usually inhabited by lynx, and may be the cause of reductions in lynx distribution through its southern range in North America, but again evidence to support this statement

is lacking. The recent invasion of Cape Breton Island by Coyotes and their access on packed roads and trails into high elevation winter habitats have been suggested as an additional potential threat to the island's lynx (M. Elderkin, personal communication; D. Banks, personal communication). However, field studies conducted where lynx and Coyote are sympatric have not identified exploitation competition between the two species (Murray and Boutin 1991; Murray et al. 1995; Staples 1995; Slough and Mowat 1996; O'Donoghue et al. 1997, 1998a).

Although purely speculative, global warming may cause reduced habitat quality for lynx by reducing snow depths, primarily at the southern edge of its range. Reduced snow depth may favour Bobcats and Coyotes over lynx in these areas.

Lynx Status and Management in Canada

Canada Lynx are listed under Appendix II of Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), primarily because it is a "look-alike" species that could be confused with other endangered felids. Global ranking assigned by The Nature Conservancy is G5 (common to very common; demonstrably secure and essentially ineradicable under present conditions). Lynx are classified as endangered or threatened in most states in the U.S., with the exception of Alaska where lynx are classified as a furbearer and trapping is permitted. Lynx south of the 49th parallel were listed as threatened in 2000 under the U.S. Endangered Species Act. Legal harvest in the contiguous states is allowed only in Montana, which has a state-wide quota of two.

The COSEWIC status assigned to lynx in 1989 was "Not At Risk" (Stardom 1989*), which was reaffirmed in 2001 (Poole 2001*). Subnational Conservation Data Centre (CDC) rankings and status designations vary (Table 1), with the greatest concern a result of reduced range, low population levels and threats to the population discussed above. Lynx harvest is regulated in each jurisdiction by provincial/territorial laws. Lynx are fully protected (including from First Nations harvesters) in only a small proportion of their range in Canada. These areas include most, but not all, national and provincial parks, and some federal lands such as military testing areas and bases, and are estimated to be less than 2–3% of lynx range in Canada.

The lynx is classified as a furbearer in all Canadian jurisdictions with the exception of British Columbia, where it is now also classified as a big game species to facilitate licensing (M. Badry, personal communication; Table 2). All jurisdictions in Canada allow harvesting of lynx, except in the Maritime Provinces. Season length varies up to five months, with the longer seasons generally occurring in the more northern jurisdictions. Most provinces vary season length during the lynx cycle, and all jurisdictions reported regulating the harvest using seasons (Table 2). Additional regulation techniques included quotas and temporary closures, either regional or jurisdiction-wide. All jurisdictions also reported monitoring the harvest by tracking harvest levels from trapper returns. Additional harvest monitoring techniques included compulsory inspections (the pelt has to be brought to wildlife official and is sealed or tagged), and compulsory reporting (the trapper has to file a report of harvest at season end). Population monitoring techniques include tracking the hare cycle (through track counts [Labonté et al. 1999*] or pellet plots [Krebs et al. 1987, 2001]), monitoring the proportion of kits in the harvest through pelt measurements (Quinn and Gardner 1984; Slough 1996) or carcass collections, and trapper questionnaires (Slough et al. 1987) which provide catch per unit effort and index population trends. Nova Scotia has been experimenting with track counts at bait sites and using aircraft to monitor lynx numbers on Cape Breton Island (M. Elderkin, personal communication).

The number of lynx taken by licensed trappers has declined since the early 1980s (Figures 2 and 3). Pelt prices peaked in the mid to late 1980s, concurrent with the low in the cycle, and declined by 80–90% through to the early 1990s. Alberta has generally produced the largest number of lynx pelts, up to one quarter to one third of the Canadian total (Table 3). Excluding the Maritime Provinces, the remaining provinces and territories each produce 8–14% of the annual harvest, with British Columbia and the Northwest Territories generally producing higher numbers than most. Harvest data are derived primarily from compulsory inspection and pelt marking or through auction house records, and can be considered to be a relatively accurate indication of actual harvest level. Game hunters in British Columbia have harvested an average of 16 lynx annually over the past 15 years (M. Badry, personal communication). The number of lynx harvested illegally is unknown but may be insignificant on a national scale, given current low fur prices and declining interest in trapping. Almost all lynx trapped in Canada are exported (Stardom 1989*). The trade in live specimens is insignificant, totalling less than 0.05% of the total harvest (Stardom 1989*).

Concern for lynx populations in most jurisdictions in Canada peaked during the 1980s when record high pelt prices coincided with the low of the cycle, trapper effort was high and overharvest was suspected in many areas (Todd 1985). Many jurisdictions enacted more restrictive legislation to curb the harvest through the late 1980s and into the low of the mid-1990s. Some jurisdictions (e.g., Québec and Manitoba) only lifted season closures in 1998 after lynx populations were into the increase phase of the cycle and the "health" of the population was perceived to be recovering. The experience of concern and reaction to perceived overharvest may result in more careful monitoring and management of lynx populations in the foreseeable future. However, given the intensity and accuracy of

TABLE 2. Legislative status, regulations, monitoring and population trend of Canada lynx by management jurisdiction in Canada based on information and opinions provided by agency biologists in fall 1999, and updated in 2003 from government websites. All jurisdictions regulated the harvest using seasons and reported monitoring harvest levels from trapper returns. Most provinces vary season length during the lynx cycle.

Province/territory	Legislative status	Maximum season	Harvest regulation and monitoring	Population monitoring	Population trend (over past two decades)
Newfoundland	Furbearer	Labrador: 15 October – 31 March Newfoundland Island: 20 October – 1 February	Compulsory inspection (Newfoundland Island)	Carcass collections, hare cycle monitoring	Stable
Nova Scotia	Furbearer	Closed	Closure	Aerial track transects, tracking at bait sites	Stable, possibly decreasing
New Brunswick	Furbearer	Closed	Closure; inspection of incidental captures	Regional study	Unknown
Québec	Furbearer	Mostly 25 October – 1 February	Quota; closure (1995–98)	Questionnaire, hare cycle monitoring	Stable
Ontario	Furbearer	25 October – 28 February	Quota; compulsory registration	Questionnaire	Unknown
Manitoba	Furbearer	1 December – 28 February	Closure (1995–98), compulsory inspection	Pelt measurement	Stable
Saskatchewan	Furbearer	1 November – 28 February	–	–	Stable
Alberta	Furbearer	1 December – 15 February	Quota, compulsory registration	–	Unknown, possibly still depressed in some stable areas
British Columbia	Furbearer, big game	15 November – 15 February	BG quota of 1, compulsory inspection in south	Pelt measurement	Stable
Yukon	Furbearer	1 November – 10 March	Compulsory inspection	–	Stable
Northwest Territories	Furbearer	1 November – 15 March	–	Pelt measurement, carcass collection, hare cycle monitoring	Unknown, likely stable
Nunavut	Furbearer	1 November – 15 March	–	–	Unknown

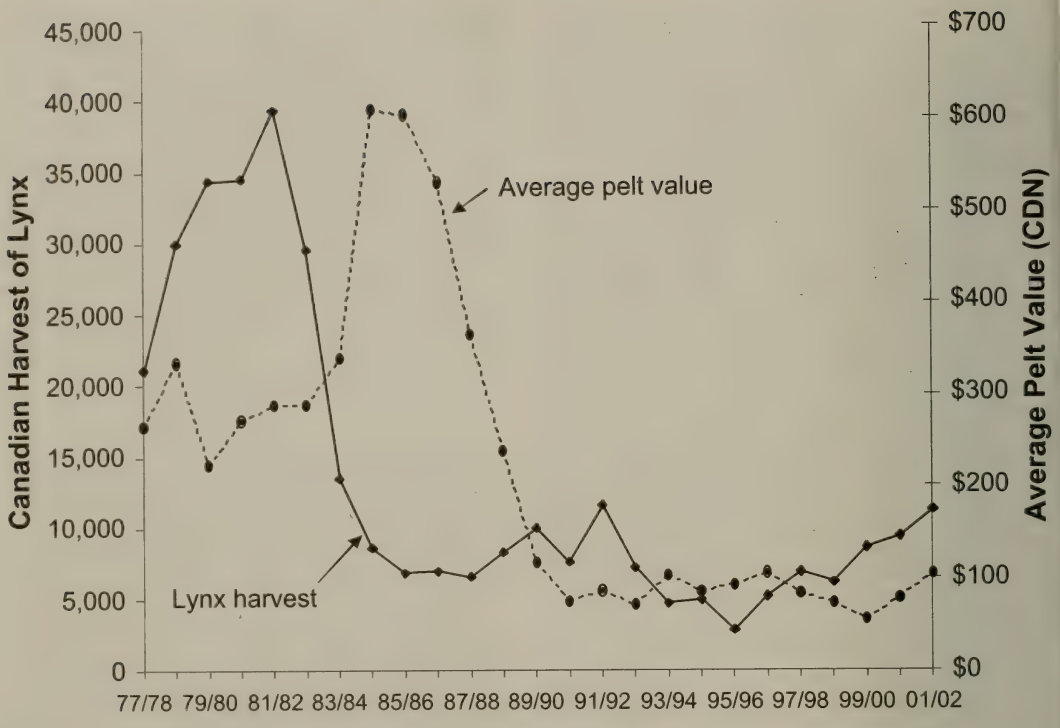


FIGURE 3. Canada Lynx harvest in Canada and average pelt value from 1977 to 2002. Data from Statistics Canada, updated to August 2003.

the current monitoring and research programs on lynx in Canada, most jurisdictions would be unable to identify anything but a dramatic decline in lynx numbers or distribution beyond the normal cyclic fluctuations.

The public generally perceives lynx as an elusive denizen of the Canadian forests. Long important to the trapping industry, the recent attention to biological diversity and conservation biology has meant that the lynx has been recognized as an important component of the ecosystem. The cyclic fluctuations in numbers and its close ties to the cyclic abundance of Snowshoe Hares have fascinated many over the years, including scientists keen on determining the driving mechanisms behind the hare and lynx cycles.

While direct assessment of lynx populations is exceedingly difficult, there is no evidence to suggest that lynx numbers across most of Canada are declining. Harvest effort and numbers have declined dramatically over the past decade, and there is little to suggest a reversal in trend. There is no evidence that illegal harvest is a serious concern. High reproductive potential and the propensity to disperse long distances suggest that lynx numbers in affected areas can be repopulated given time and removal of the factors that cause the initial decrease. Lynx habitat should be maintained given continuing availability of early to mid-seral stage forests with adequate structure for denning and cover.

Acknowledgments

I thank COSEWIC, Canadian Wildlife Service for funding the preparation the full status report submitted to them and M. Festa-Bianchet for administrating the work and fielding countless questions. Page charges for this review were covered by Resources, Wildlife and Economic Development, Government of the Northwest Territories. Numerous people provided information and advice from all jurisdictions. G. Mowat kindly reviewed an earlier draft, and I received additional comments from members of the COSEWIC Terrestrial Mammals Specialist Group (M. Festa-Bianchet, J. Murie, D. Nagorsen, M. Crête, T. Herman, and M. Brigham) and an anonymous reviewer. I benefited greatly from involvement in the preparation of Mowat et al. (2000), and I thank my co-authors G. Mowat and M. O'Donoghue. The opinions presented here are solely mine, and do not necessarily represent those of COSEWIC.

Documents Cited (marked * in the text)

Labonté, J., F. Potvin, J. P. Ouellet, and **J. Ferron.** 1999. Analyse d'inventaires de pistes de lynx du Canada dans cinq secteurs du Québec et proposition de deux approches

TABLE 3. Provincial and territorial harvest records for Canada Lynx, 1983–2002. Source: Statistics Canada (August 2003).

	83/84	84/85	85/86	86/87	87/88	88/89	89/90	90/91	91/92	92/93	93/94	94/95	95/96	96/97	97/98	98/99	99/00	00/01	01/02
Nfld	425	469	297	114	76	53	46	34	108	115	78	61	49	58	89	91	121	191	633
PEI																			
NS	5	6	8									2					11		
NB																			
Que	1735	1799	1261	1011	880	847	839	699	978	1176	924	965	139	85	635	1105	1482	1884	3588
Ont	1677	495	675	508	512	573	526	665	932	929	812	991	527	734	830	655	635	1004	1343
Man	596	419	29	400	383	406	446	372	530	356	244	195	78	95	127	246	275	454	575
Sask	932	560	610	674	157	0	385	581	1129	639	613	558	365	724	746	812	1229	1661	1763
Alta	3054	1279	813	854	617	720	1807	1278	2215	1391	773	786	591	1365	2460	1438	1456	2028	1667
BC	2760	1668	1206	1050	1113	1243	1230	600	2017	1172	750	641	382	717	533	500	602	701	864
Yukon	961	925	805	668	799	1235	1875	1256	1403	529	100	187	152	310	442	592	459	603	214
NWT	1300	1005	1149	1674	2037	3188	2823	2094	2230	873	419	521	536	1083	1011	709	2303	835	579
CANADA	13445	8625	6853	6953	6574	8265	9977	7579	11542	7180	4713	4907	2819	5171	6873	6148	8573	9361	11226
Ave. value	$340.92	$611.38	$605.23	$531.37	$365.44	$238.04	$117.44	$75.51	$86.57	$71.22	$103.51	$86.01	$93.05	$106.04	$84.95	$72.70	$55.10	$78.68	$104.33

applicables à un programme de suivi. Direction de la faune et des habitats. Ministère de l'Environnement et de la Faune, Québec, Canada.

Poole, K. G. 2001. COSEWIC status report on Canada lynx (*Lynx canadensis*). Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada.

Stardom, R. 1989. Status report on the lynx *Lynx canadensis* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada.

Stephenson, R. O. 1986. Development of lynx population estimation techniques. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Report, Project W-22-5, Job 7.12R. Juneau, Alaska, USA.

Literature Cited

Apps, C. D. 2000. Space-use, diet, demographics, and topographic associations of lynx in the southern Canadian Rocky Mountains: a study. Pages 351–371 *in* Ecology and conservation of lynx in the United States. *Edited by* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. University Press of Colorado, Boulder, Colorado, USA.

Aubry, K. B., G. M. Koehler, and **J. R. Squires.** 2000. Ecology of Canada lynx in the southern boreal forests. Pages 373–396 *in* Ecology and conservation of lynx in the United States. *Edited by* L. F. Ruggiero K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. University Press of Colorado, Boulder, Colorado, USA.

Bailey, R. G. 1998. Ecoregions map of North America: Explanatory note. Miscellaneous Publications Number 1548. USDA Forest Service, Washington, D.C.

Bailey, T. N. 1974. Social organization in a bobcat population. Journal of Wildlife Management 38: 435–446.

Bailey, T. N., E. E. Bangs, M. F. Portner, J. C. Malloy, and **R. J. McAvinchey.** 1986. An apparent overexploited lynx population in the Kenai Peninsula, Alaska. Journal of Wildlife Management 50: 279–290.

Banfield, A. W. F. 1974. The mammals of Canada. University of Toronto Press, Toronto, Ontario, Canada.

Banville, D. 1986. Étude écologique du lynx du Canada sur la haute Côte-Nord. Québec Ministère du Loiser, de la Chasse et de la Pêche, Québec, Canada.

Beltrán, J. F., J. E. Rice, and **R. L. Honeycutt.** 1996. Taxonomy of the Iberian lynx. Nature 379: 407–408.

Berrie, P. M. 1974. Ecology and status of the lynx in interior Alaska. Pages 4–41 *in* The world's cats. Volume 1. *Edited by* R. L. Eaton. World Wildlife Safari, Winston, Oregon, USA.

Bergerud, A. T. 1971. The population dynamics of the Newfoundland caribou. Wildlife Monographs 25: 1–55.

Boutin, S., C. J. Krebs, R. Boonstra, M. R. T. Dale, S. J. Hannon, K. Martin, A. R. E. Sinclair, J. N. M. Smith, R. Turkington, M. Blower, A. Byrom, F. I. Doyle, C. Doyle, D. Hik, L. Hofer, A. Hubbs, T. Karels, D. L. Murray, V. Nams, M. O'Donoghue, C. Rohner, and **S. Schweiger.** 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. Oikos 74: 69–80.

Brainerd, S. M. 1985. Reproductive ecology of bobcats and lynx in western Montana. M.S. thesis, University of Montana. Missoula, Montana, USA. 85 pages.

Brand, C. J., L. B. Keith, and **C. A. Fischer.** 1976. Lynx responses to changing snowshoe hare densities in Alberta. Journal of Wildlife Management 40: 416–428.

Brand, C. J., and **L. B. Keith.** 1979. Lynx demography during a snowshoe hare decline in Alberta. Journal of Wildlife Management 43: 827–849.

Brittell, J. D., R. J. Poelker, S. J Sweeney, and **G. M. Koehler.** 1989. Native cats of Washington. Section III: Lynx. Washington Department of Wildlife, Olympia, Washington, USA.

Buskirk, S. W., L. F. Ruggiero, and **C. J. Krebs.** 2000. Habitat fragmentation and interspecific competition: implications for lynx conservation. Pages 83–100 *in* Ecology and conservation of lynx in the United States. *Edited by* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. University Press of Colorado, Boulder, Colorado, USA.

Butler, L. 1953. The nature of cycles in populations of Canadian mammals. Canadian Journal of Zoology 31: 242–262.

Canadian Endangered Species Conservation Council (CESCC). 2001. Wild species 2000: the general status of species in Canada. Minister of Public Works and Government Services Canada, Ottawa, Canada.

Carbyn, L. N., and **D. Patriquin.** 1983. Observations on home range sizes, movements and social organization of lynx, *Lynx canadensis*, in Riding Mountain National Park, Manitoba. Canadian Field-Naturalist 97: 262–267.

Chubbs, T. E., and **F. R. Phillips.** 1993. An apparent longevity record for Canada lynx, *Lynx canadensis*, in Labrador. Canadian Field-Naturalist 107: 367–368.

de Vos, A., and **S. E. Matel.** 1952. The status of the lynx in Canada, 1929-1952. Journal of Forestry 50: 742–745.

Dwyer, P. M., F. F. Mallory, and **J. R. Pitblado.** 1989. Preliminary assessment of lynx habitat and distribution during cyclic population lows in northern Ontario. Musk-ox 37: 129–136.

Elton, C., and **M. Nicholson.** 1942. The ten year cycle in numbers of lynx in Canada. Journal of Animal Ecology 11: 215-244.

Fortin, C., and **J. Huot.** 1995. Ecologie comparée du Coyote, du Lynx du Canada et du Renard roux au parc national Forillon. Rapport Final for Parcs Canada, Département de Biologie, Université Laval, Québec, Canada.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior 28: 1140–1162.

Hall, E. R. 1981. Mammals of North America. Second edition. John Wiley and Sons, New York, N.Y., USA. 1181 pp.

Hatler, D. F. 1988. A lynx management strategy for British Columbia. Wildlife working report WR-34. B.C. Ministry of Environment and Parks, Victoria, B.C., Canada.

Hodges, K. E. 2000a. The ecology of snowshoe hares in northern boreal forests. Pages 117–161 *in* Ecology and conservation of lynx in the United States. *Edited by* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. University Press of Colorado, Boulder, Colorado, USA.

Hodges, K. E. 2000b. Ecology of snowshoe hares in southern boreal and montane forests. Pages 163–206 *in* Ecology and conservation of lynx in the United States. *Edited by* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. University Press of Colorado, Boulder, Colorado, USA.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. American Midland Naturalist 63: 152–161

Johnson, W. N., T. F. Paragi, and **D. D. Katnik.** 1995. The relationships of wildland fire to lynx and marten populations and habitat in interior Alaska. Final Report. U.S. Fish and Wildlife Service, Galena, Alaska, USA.

Keith, L. B. 1963. Wildlife's ten-year cycle. University of Wisconsin Press, Madison, Wisconsin, USA.

Keith, L. B., A. W. Todd, C. J. Brand, R. S. Adamcik, and **D. H. Rusch.** 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. Proceedings of the International Congress of Game Biologists 13: 151–175.

Kelsall, J., E. S. Telfer, and **T. D. Wright.** 1977. The effects of fire on the ecology of the boreal forest, with particular reference to the Canadian north: a review and selected bibliography. Canadian Wildlife Service, Occasional Paper Number 32, Ottawa, Ontario, Canada.

Kesterson, M. B. 1988. Lynx home range and spatial organization in relation to population density and prey abundance. M.S. thesis, University of Alaska, Fairbanks, Alaska, USA.

Koehler, G. M. 1990. Population and habitat characteristics of lynx and snowshoe hares in north central Washington. Canadian Journal of Zoology 68: 845–853.

Koehler, G. M., and **K. B. Aubry.** 1994. Lynx. Pages 74–98 *in* The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. *Edited by* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski. U. S. Forest Service General Technical Report RM-254.

Krebs, C. J., G. S. Gilbert, S. Boutin, and **R. Boonstra.** 1987. Estimation of snowshoe hare population density from turd transects. Canadian Journal of Zoology 65: 565–567.

Krebs, C. J., R. Boonstra, V. Nams, M. O'Donoghue, K. E. Hodges, and **S. Boutin.** 2001. Estimating snowshoe hare population density from pellet plots: a further evaluation. Canadian Journal of Zoology 79: 1–4.

Kurtén, B., and **R. Rausch.** 1959. Biometric comparisons between North American and European mammals. II. A comparison between the northern lynxes of Fennoscandia and Alaska. Acta Arctica 11: 21–45.

Legendre, P., F. Long, R. Bergeron, and **J-M. Levasseur.** 1978. Inventaire aérien de la faune dans le Moyen Nord québécois. Canadian Journal of Zoology 56: 451–462.

Litvaitis, J. A., D. Kingman, Jr., and **E. Orff.** 1991. Status of lynx in New Hampshire. Transactions of the Northeast Section of the Wildlife Society 48: 70–75.

McCord, C. M., and **J. E. Cardoza.** 1982. Bobcat and lynx. Pages 728–766 *in* Wild mammals of North America. *Edited by* J. A. Chapman and G. A. Feldhamer. The Johns Hopkins University Press, Baltimore, Maryland, USA.

McKelvey, K. S., K. B. Aubry, and **Y. K. Ortega.** 2000. History and distribution of lynx in the contiguous United States. Pages 207–264 *in* Ecology and conservation of lynx in the United States. *Edited by* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. University Press of Colorado, Boulder, Colorado, USA.

Maj, M., and **E. O. Garton.** 1994. Fisher, lynx, wolverine summary of distribution information. Pages 169–175 *in* The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. *Edited by* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski. U. S. Forest Service General Technical Report RM-254.

Major, A. R. 1989. Lynx, *Lynx canadensis canadensis* (Kerr) predation patterns and habitat use in the Yukon Territory, Canada. M.S. thesis, State University of New York, Syracuse, New York, USA.

Mech, L. D. 1973. Canada lynx invasion of Minnesota. Biological Conservation 5: 151–152.

Mech, L. D. 1977. Record movement of a Canadian lynx. Journal of Mammalogy 58: 676–677.

Mellen, J. D. 1993. A comparative analysis of scent-marking, social and reproductive behavior in 20 species of small cats (*Felis*). American Zoologist 33: 151–166.

Mowat, G. 1993. Lynx recruitment in relation to snowshoe hare density. M.S. thesis, University of Alberta, Edmonton, Canada.

Mowat, G., S. Boutin, and **B. G. Slough.** 1996a. Using placental scars to estimate litter size and pregnancy rate in lynx. Journal of Wildlife Management 60: 430–440.

Mowat, G., B. G. Slough, and **S. Boutin.** 1996b. Lynx recruitment during a snowshoe hare population peak and decline in southwest Yukon. Journal of Wildlife Management 60: 441–452.

Mowat, G., and **B. G. Slough.** 1998. Some observations on the natural history and behaviour of the Canada lynx, *Lynx canadensis*. Canadian Field-Naturalist 112: 32–36.

Mowat, G., K. G. Poole, and **M. O'Donoghue.** 2000. Ecology of lynx in northern Canada and Alaska. Pages 265–306 *in* Ecology and conservation of lynx in the United States. *Edited by* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. University Press of Colorado, Boulder, Colorado, USA.

Mowat, G., and **B. G. Slough.** 2003. Habitat preference of Canada lynx through a cycle in snowshoe hare abundance. Canadian Journal of Zoology 81: 1736–1745.

Murray, D. L., and **S. Boutin.** 1991. The influence of snow on lynx and coyote movements: does morphology effect behavior? Oecologia 88: 463–469.

Murray, D. L., S. Boutin, and **M. O'Donoghue.** 1994. Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. Canadian Journal of Zoology 72: 1444–1451.

Murray, D. L., S. Boutin, M. O'Donoghue, and **V. O. Nams.** 1995. Hunting behaviour of a sympatric felid and canid in relation to vegetative cover. Animal Behaviour 50: 1203–1210.

Nellis, C. H., S. P. Wetmore, and **L. B. Keith.** 1972. Lynx-prey interactions in central Alberta. Journal of Wildlife Management 36: 320–329.

Noiseux, F., and **G. J. Doucet.** 1987. Étude de la population du lynx du Canada (*Lynx canadensis*) de la Réserve Faunique des Laurentides, Québec. Québec Ministère du Loisir, de la Chasse et de la Pêche, Québec, Canada.

Nowell, K., and **P. Jackson.** 1996. Wild Cats: status survey and conservation action plan. IUCN/SSC Cat Specialist Group, Gland, Switzerland.

O'Brien, S. J. 1996. Molecular genetics and phylogenetics of the Felidae. Pages xxii–xxiv *in* Wild Cats: status survey and conservation action plan. *Edited by* K. Nowell and P. Jackson. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.

O'Connor, R. M. 1984. Population trends, age structure and reproductive characteristics of female lynx in Alaska, 1963 through 1973. M.S. thesis, University of Alaska, Fairbanks, Alaska, USA.

O'Donoghue, M., E. Hofer, and **F. I. Doyle.** 1995. Predator versus predator. Natural History 104(3): 6–9.

O'Donoghue, M., S. Boutin, C. J. Krebs, and **E. J. Hofer.** 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. Oikos 80: 150–162.

O'Donoghue, M., S. Boutin, C. J. Krebs, D. L. Murray, and **E. J. Hofer.** 1998a. Behavioural responses of coyotes and lynx to the snowshoe hare cycle. Oikos 82: 169–183.

O'Donoghue, M., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and **E. J. Hofer.** 1998b. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology 79: 1193–1208.

O'Donoghue, M., S. Boutin, D. L. Murray, C. J. Krebs, E. J. Hofer, U. Breitenmoser, C. Breitenmoser-Würsten, G. Zuleta, C. Doyle, and **V. O. Nams.** 2001. Coyotes and lynx. Chapter 13 *in* Ecosystem dynamics in the boreal forest: the Kluane Project. *Edited by* C. J. Krebs, S. Boutin, and R. Boonstra. Oxford University Press.

Paragi, T. F., W. N. Johnson, and **D. D. Katnik.** 1997. Selection of post-fire seres by lynx and snowshoe hares in the Alaskan taiga. Northwest Naturalist 78: 77–86.

Parker, G. R. 1981. Winter habitat use and hunting activities of lynx (*Lynx canadensis*) on Cape Breton Island, Nova Scotia. Pages 221-248 *in* Worldwide Furbearer Conference proceedings, Aug. 3–11, 1980. *Edited by* J. A. Chapman, and D. Pursley. Frostburg, Maryland, USA.

Parker, G. R., J. W. Maxwell, L. D. Morton, and **G. E. J. Smith.** 1983. The ecology of the lynx (*Lynx canadensis*) on Cape Breton Island. Canadian Journal of Zoology 61: 770–786.

Perham, C. T. 1995. Home range, habitat selection, and movements of lynx in eastern interior Alaska. M. Sc. thesis. University of Alaska, Fairbanks.

Perham, C., T. Doyle, and **B. Route.** 1993. Mortality factors, home range characteristics, and habitat preferences of lynx inhabiting Tetlin National Wildlife Refuge and Wrangell-St. Elias National Park and Preserve. U.S. Fish and Wildlife Service, Tetlin National Wildlife Refuge, Tok, Alaska, USA.

Poole, K. G. 1994. Characteristics of an unharvested lynx population during a snowshoe hare decline. Journal of Wildlife Management 58: 608–618.

Poole, K. G. 1995. Spatial organization of a lynx population. Canadian Journal of Zoology 73: 632–641.

Poole, K. G. 1997. Dispersal patterns of lynx in the Northwest Territories. Journal of Wildlife Management 61: 497–505.

Poole, K. G., L. A. Wakelyn, and **P. N. Nicklen.** 1996. Habitat selection by lynx in the Northwest Territories. Canadian Journal of Zoology 74: 845–850.

Powell, R. A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. Zoologica Tierpsychologica 50: 153–165.

Quinn, N. W. S., and **J. F. Gardner.** 1984. Relationships of age and sex to lynx pelt characteristics. Journal of Wildlife Management 48: 953–956.

Quinn, N. W. S., and **G. Parker.** 1987. Lynx. Pages 683–694 *in* Wild furbearer management and conservation in North America. *Edited by* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch. Ontario Trappers Association, North Bay, Ontario, Canada.

Quinn, N. W. S., and **J. E. Thompson.** 1987. Dynamics of an exploited Canada lynx population in Ontario. Journal of Wildlife Management 51: 297–305.

Saunders, J. K. 1963a. Food habits of lynx in Newfoundland. Journal of Wildlife Management 27: 384–390.

Saunders. J. K. 1963b. Movements and activities of lynx in Newfoundland. Journal of Wildlife Management 27: 390–400.

Seidensticker, J. C., IV, M. G. Hornocker, W. V. Wiles, and **J. P. Messick.** 1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monographs 35: 1–60.

Seton, E. T. 1929. Lives of game animals. Doubleday, Doran & Company, New York, N.Y., USA.

Slough, B. G., R. H. Jessup, D. I. McKay, and **A. B. Stephenson.** 1987. Wild furbearer management in western and northern Canada. Pages 1062–1076 *in* Wild furbearer management and conservation in North America. *Edited by* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch. Ontario Trappers Association, North Bay, Ontario, Canada.

Slough, B. G. 1996. Estimating lynx population age ratio with pelt length data. Wildlife Society Bulletin 24: 495–499.

Slough, B. G. 1999. Characteristics of Canada lynx, *Lynx canadensis*, maternal dens and denning habitat. Canadian Field-Naturalist 113: 605–608.

Slough, B. G., and **G. Mowat.** 1996. Population dynamics of lynx in a refuge and interactions between harvested and unharvested populations. Journal of Wildlife Management 60: 946–961.

Smith, C. H. 1983. Spatial trends in Canadian snowshoe hare, *Lepus americanus*, population cycles. Canadian Field-Naturalist 97: 151-160.

Smith, J. D., E. M. Addison, D. G. Joachim, and **L. M. Smith.** 1986. Helminth parasites of Canada lynx (*Felis canadensis*) from northern Ontario. Canadian Journal of Zoology 64: 358–364.

Staples, W. R. 1995. Lynx and coyote diet and habitat relationships during a low hare population on the Kenai Peninsula, Alaska. M.S. thesis, University of Alaska, Fairbanks, Alaska, USA.

Stephenson, R. O., D. V. Grangaard, and **J. Burch.** 1991. Lynx, *Felis lynx*, predation on Red Foxes, *Vulpes vulpes*, Caribou, *Rangifer tarandus*, and Dall Sheep, *Ovis dalli*, in Alaska. Canadian Field-Naturalist 105: 255–262.

Thompson, I. D. 1988. Habitat needs of furbearers in relation to logging in boreal Ontario. The Forestry Chronicle 64: 251–261.

Thompson, I. D., I. J. Davidson, S. O'Donnell, and **F. Brazeau.** 1989. Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. Canadian Journal of Zoology 67: 1816–1823.

Todd, A. W. 1985. The Canada lynx: ecology and management. Canadian Trapper 13: 15–20.

Tumlison, R. 1987. *Felis lynx*. Mammalian Species 269: 1–8.

van Zyll de Jong, C. G. 1966a. Parasites of the Canada lynx, *Felis (Lynx) canadensis* (Kerr). Canadian Journal of Zoology 44: 499–509.

van Zyll de Jong, C. G. 1966b. Food habits of the lynx in Alberta and the Mackenzie District, N. W. T. Canadian Field-Naturalist 80: 18–23.

van Zyll de Jong, C. G. 1971. The status and management of the Canada lynx in Canada. Pages 16-22 *in* Symposium on the native cats of North America. *Edited by* S. E. Jorgensen and L. D. Mech. U.S. Bureau of Sports Fish and Wildlife, Federal Building, Fort Snelling, Twin Cities, Minnesota, USA.

van Zyll de Jong, C. G. 1975. Differentiation of the Canada lynx, *Felis (Lynx) canadensis subsolana*, in Newfoundland. Canadian Journal of Zoology 53: 699–705.

Viereck, L. A. 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. Pages 201-220 *in* The role of fire in northern circumpolar ecosystems. *Edited by* R. W. Wein and D. A. MacLean. John Wiley and Sons, Toronto, Ontario, Canada.

Ward, R. M. P., and **C. J. Krebs.** 1985. Behavioural responses of lynx to declining snowshoe hare abundance. Canadian Journal of Zoology 63: 2817–2824.

Werdelin, L. 1981. The evolution of lynxes. Annales Zoologica Fennici 18: 37–71.

Werdelin, L. 1983. Small Pleistocene felines of North America. Journal of Vertebrate Paleontology 5: 194–210.

Werdelin, L. 1996. The history of Felid classification. Pages xviii–xxiii *in* Wild cats: status survey and conservation action plan. *Edited by* K. Nowell and P. Jackson. International Union for the Conservation of Nature and Natural resources, Gland, Switzerland.

Wolff, J. O. 1994. More on juvenile dispersal in mammals. Oikos 71: 349–352.

Wozencraft, W. C. 1993. Order Carnivora. Pages 286–346 *in* Mammal species of the world, second edition. *Edited by* D. E. Wilson and D. M. Reeder. Smithsonian Institution, Washington, D.C., USA.

Received 20 July 2001
Accepted 20 December 2003

Ecological Aspects of a Wood Turtle, *Glyptemys insculpta*, Population at the Northern Limit of its Range in Québec

Andrew D. Walde[1,2,3], J. Roger Bider[1], Claude Daigle[4], Denis Masse[5], Jean-Claude Bourgeois[6], Jacques Jutras[7], and Rodger D. Titman[2]

[1] St. Lawrence Valley Natural History Society, 21125 chemin Ste.-Marie, Ste.-Anne-de-Bellevue, Québec, H9X 3Y7 Canada
[2] Department of Natural Resources, Macdonald Campus of McGill University, 21111 Lakeshore Road, Ste.-Anne-de-Bellevue, Québec H9X 3V9 Canada
[3] Corresponding author: P. O. Box 36, Helendale, California 92342 Email: awalde@hotmail.com
[4] Société de la faune et des parcs du Québec, Direction de la recherche sur la faune, 675, boulevard René-Lévesque Est, Québec, Québec G1R 5V7 Canada
[5] Parcs Canada, Parc national de la Mauricie, 2141, chemin Saint-Paul, Saint-Mathieu-du-Parc, Québec G0X 1N0 Canada
[6] Société de la faune et des parcs du Québec, Direction de l'aménagement de la faune de la Mauricie, 5575, rue Saint-Joseph, Trois-Rivières, Québec G8Z 4L7 Canada
[7] Société de la faune et des parcs du Québec, Direction du développement de la faune, 675, boulevard René-Lévesque Est, Québec, Québec G1R 5V7 Canada

Walde, Andrew D., J. Roger Bider, Claude Daigle, Denis Masse, Jean-Claude Bourgeois, Jacques Jutras, and Rodger D. Titman. 2003. Ecological aspects of a Wood Turtle, *Glyptemys insculpta*, population at the northern limit of its range in Québec. Canadian Field-Naturalist 117(3): 377-388.

As part of a conservation research initiative, a population of Wood Turtles (*Glyptemys insculpta*) at the northern limit of its range was studied to ascertain characteristics of its demographics, morphometrics, density, mortality, feeding, and mating activities. Turtles were captured and marked during the activity period in 1996 and 1997. In addition, 20 individuals were radio-tracked weekly. A total of 188 turtles was captured and the size of the population in the study area was estimated at 238 turtles. The estimated population density based on this calculation is 0.44 turtles/ha. This is less than other studies indicating that population densities are greater in southern populations. Turtles from this population were large (carapace length of males=214.5 ± 4.21 mm, females=201.1 ± 10.88 mm) which supports the hypothesis that turtle size is negatively correlated with number of frost free days. The sex ratio was not significantly different from 1:1. Juvenile turtles accounted for 31.4% of the population. Observations of feeding habits support the claim that Wood Turtles are opportunistic omnivores. Of the 35 mating or courtship events observed, 77 % occurred in the fall and half of them between 11:00 and 13:00. Although limb and tail injuries and parasites were observed on many turtles, no dead turtles were observed. This last result, combined with the high rate of recruitment and even sex ratio suggests that this population is stable, making it an ideal population with which to make comparisons with other studies in areas where the species could be in decline.

Key Words: Wood Turtle, *Glyptemys insculpta,* Emydidae, morphology, density, ecology, Québec.

The Wood Turtle, *Glyptemys insculpta*, ranges throughout the northeastern United States and southeastern Canada, from central Ontario, east to Nova Scotia, and south to Virginia (Ernst et al. 1994). Wood Turtle populations are scattered and disjunct throughout their distribution (Ernst 2001a; Niederberger and Seidel 1999) and it is thought that there is little chance now of interpopulation exchange or natural recolonization into areas from which they have been extirpated (Harding and Bloomer 1979; R. Brooks personal communication). In southern Québec, Wood Turtles are considered to be widespread, but uncommon, up to 47° north latitude (Beaulieu 1992; Bider and Matte 1996; Daigle 1997).

In 1992, *Glyptemys insculpta* (as *Clemmys insculpta*) was listed in Appendix II of the Convention on the International Trade of Endangered Species of Flora and Fauna (CITES) (Buhlmann 1992, 1993). Currently, the Wood Turtle is listed as threatened, endangered, or protected by law in most of the U.S. states within its range (Harding 1991*; Klemens 1992*; Buhlmann 1993; Levell 2000). In Canada, this species has been assigned the status of "vulnerable" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Green 1996; Litzgus and Brooks 1996*). In Québec, the Wood Turtle was included on a list of species susceptible to being declared vulnerable or threatened (Beaulieu 1992). A recent status report on the Wood Turtle in Québec recommended a status of vulnerable (Galois and Bonin 1999), although no legal status has been assigned.

Recent studies have indicated that many Wood Turtle populations have undergone significant declines (Harding and Bloomer 1979; Garber 1989; Harding 1990; Ernst et al. 1994; Gilhen et al. 1994*; Garber and Burger 1995; Niederberger and Seidel 1999; Ron

Brooks personal communication). Some of these authors have suggested that collection for the pet trade is the single greatest cause for "population crashes", and have made conservation recommendations e.g. Litzgus and Brooks 1996*) which advocate not revealing any exact location. Many of these authors admit that habitat loss and fragmentation contribute significantly to declines as well. Ernst (2001a) states that habitat destruction and alteration are the most serious problems facing Wood Turtles. Levell (2000), in a review of the pet trade, argues that this may not be as widespread a problem as has been sometimes indicated for the Wood Turtle. He suggests that increased human population pressures such as road mortality and habitat fragmentation, degradation and destruction are the most serious threats. Although it is difficult to assess habitat decay and the subsequent decline of a species without long-term studies, one study in Québec documented the effect of present agricultural practices. These were shown to be causing decreased recruitment into the population and an increased rate of injuries, mutilations and even death in adults (Saumure and Bider 1998). Another study, in Connecticut, concluded that human recreational activities caused the extirpation of two populations (Garber and Burger 1995).

There have been numerous studies on Wood Turtles which have examined habitat requirements, home range, daily activities, reproduction, dominance and habitat use (Powell 1967; Carroll and Ehrenfeld 1978; Ernst 1986; Lovich et al. 1990; Brewster and Brewster 1991; Ross et al. 1991; Quinn and Tate 1991; Brooks et al. 1992; Kaufmann 1992, 1995). The most complete studies of ecology and life histories are those of Harding and Bloomer (1979) in Michigan and New Jersey, and Farrell and Graham (1991) in New Jersey. More detailed studies of Wood Turtle life histories must be conducted (Harding and Bloomer 1979; Farrell and Graham 1991; Ross et al. 1991; Brooks et al. 1992; Litzgus and Brooks 1996*; Saumure 1997*; Ernst 2001b). That this data-base is still inadequate is demonstrated by a management recommendation from the COSEWIC report that further studies of Canadian Wood Turtle populations need to be started or expanded (Litzgus and Brooks 1996*).

The objectives of this study were to gather base line data on morphometrics, density, feeding, mating, predation, and parasites from a population at the northern limit of the Wood Turtle's range in Québec. Results were then compared with published data from more southerly populations. Information concerning characteristics from a northern population are important in the planning and application of conservation and management strategies for this species.

Materials and Methods

Turtles were located and marked from May to October of 1996 and 1997 along a 7.05 km section of a meandering river and the surrounding habitats in Municipalité Régionale de Comté (MRC) Le Centre de la Mauricie, Québec, Canada (46°N, 73°W). Some of the tributary creeks and gravel roads in the general area were also surveyed. The total area over which turtles were captured was 538 ha. During May of 1996 and 1997, an intense search of the study area was undertaken to locate and mark Wood Turtles. This was accomplished by canoeing and walking along the river and hand capturing or dip-netting the turtles.

The geology of the area is that of an esker (Allard 1978*); gravel and sand with exposed granitic outcrops. The river is between 5 and 10 m wide and 0.1-2 m deep, depending on the season and precipitation patterns. The river bottom is sandy with gravel deposits. The flood plain is predominantly Speckled Alder (*Alnus rugosa*) thicket, with several ox-bow lakes and Beaver (*Castor canadensis*) ponds. Vegetation beyond the flood plain is at the border of the boreal/Great Lakes St. Lawrence Lowland forest (Farrar 1995) with White Spruce (*Picea glauca*), White Birch (*Betula papyrifera*), and Trembling Aspen (*Populus tremuloides*) dominating with some maple species (*Acer* spp.) also present. The number of frost free days (FFD) in this area was 100 (Wilson 1971). Most of the land in the study area was privately owned and had little to no development on it, although logging and aggregate mining have historically been and continue to be economic factors. The number of summer homes in the area was increasing.

For each turtle captured, date, time, location, behaviour (e.g. basking, feeding), weather, and temperature were recorded. The maximum straight line carapace (CL) and plastron lengths (PL) were measured using vernier calipers (forester type, ± 1 mm, Haglof, Sweden) and the turtle was weighed using spring scales (Pesola, ± 50 g or ± 10 g, Switzerland). Adult turtles were sexed using characteristics of length of carapace and the presence or absence of male secondary sexual characteristics, males exhibiting plastron concavity and a longer, thicker, preanal tail (Wright 1918; Harding and Bloomer 1979). Female turtles were palpated for the presence of eggs. Turtles below a minimum size were considered to be immature (minimum size was determined from results).

Age was determined by counting growth annuli, starting from the flat hatchling section and proceeding outward. This method is considered a reliable estimator of age until approximately 15-20 years of age for Wood Turtles, after which it is thought to be less reliable as the smaller annuli are too difficult to count, especially in the field (Harding and Bloomer 1979; Harding 1985*; Lovich et al. 1990). At our northern location, the growing season is short and not interrupted by aestivation; therefore, only one annulus would be expected per year. The minimum age of a Wood Turtle was assessed by counting all discernable annuli. Limb and tail injuries were recorded, as well as presence/absence of parasites and shell abnormal-

ities. Posterior carapace marginal scutes were marked for later individual identification (Cagle 1939), using a 6 mm rat-tail file that made permanent U-shaped notches, with a numbering system adapted by Saumure (1995*) from one described by Froese and Burghardt (1975).

Radio transmitters (Holohil AI-2m(4) with batteries lasting two years) were installed in May of 1996. As many as 20 turtles were monitored weekly in both years of the study until hibernation had begun. In 1997, turtles were located daily from 26 May until the end of June to aid in locating nesting sites. Radio transmitters were encased in a piece of brass pipe with a 30 cm whip antenna. A transmitter was attached to each turtle by drilling two holes in the marginal scutes and bolting it on. Transmitters were attached well off center near the posterior on males and centered at the front on females.

Results from telemetry and visual surveys indicated that these turtles rarely went outside the study area. Immigration and emigration were considered to be almost non-existent; therefore, population estimates were calculated using the Lincoln-Peterson method (Lindeman 1990; Pollock et al. 1990).

Differences between sexual and morphological parameters were tested for using the Student's *t*-test and chi-square (χ^2). Correlations among populations were analyzed using SigmaPlot 8.02 statistical software (SPSS Inc. 2002). Statistical significance was accepted at $P<0.05$.

Results

Population Structure

A total of 188 Wood Turtles (55 males, 83 females, and 50 immatures) was captured and marked during 1996 and 1997. The size of the population was estimated at 238 turtles (95% confidence limits 191-285) using the Lincoln-Peterson index. The estimated density based on this calculation is 0.44 turtles/ha.

The sex ratio of all turtles captured was 1 : 1.51, males to females (55 males: 83 females) which is significantly different from one to one ($\chi^2=5.7$, $P<0.05$). This, however, represents a biased sample as 29 females were first captured at nesting areas. The removal of these females gives a 1.0 : 0.98, male to female adult sex ratio (55 males : 54 females) which is not significantly different from 1 : 1 ($P>0.05$).

Fifty immature turtles (31.4% of 159) were captured during the study (Figures 1, 2). The results of spring surveys in May (1996 and 1997) revealed a ratio of adult to immature captures of approximately 4 : 1. A less intense survey in the fall of 1997 revealed a 2 : 1, adult to immature capture ratio, which is significantly different from the spring ratio ($\chi^2=4.34$, $p<0.05$).

Immature turtles were categorized by being smaller than the smallest recorded male or female, with adults exhibiting secondary sexual characteristics (males) or being gravid (females). The smallest male as determined by secondary sexual characteristics had a CL of 170 mm (Figure 1) and also had the fewest annuli of any distinguishable male, 11 (Figure 2). The smallest gravid female had a CL of 181 mm and 20 annuli. The youngest female known to be gravid had a CL of 203 mm and 14 annuli.

The smallest male observed courting or mating had a CL of 205 mm and 15 annuli; the smallest female observed in these activities had a CL of 188 mm and 14 annuli. It is not known whether this turtle became gravid.

Males were significantly larger than females for measurements of mean CL and weight but not for PL (Table 1). The mean numbers of annuli for males and females were not significantly different ($P>0.05$) (Table 1). One female turtle had 33 countable annuli. Age frequency distribution is represented in Figure 2.

Dietary Habits

Feeding was observed several times during the active months, except October. Turtles were seen eat-

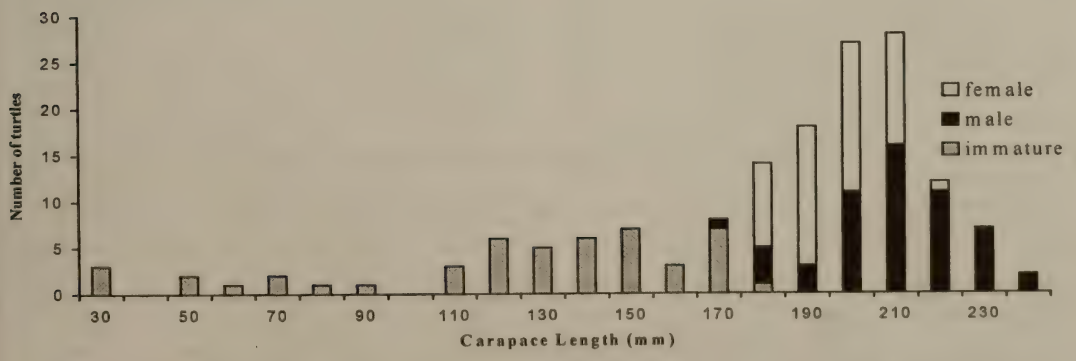


FIGURE 1. Population size structure (carapace length in mm) of 156 Wood Turtles captured from Municipalité Régionale de Comté Le centre de la Mauricie, Québec, Canada in 1996 and 1997. Turtles captured by biased sampling techniques (i.e. at nesting areas) have not been included.

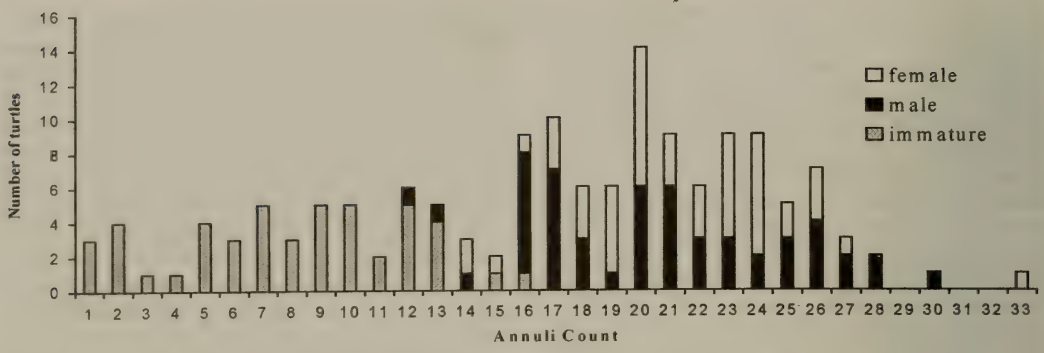


FIGURE 2. Population age structure (annuli count) of 153 Wood Turtles captured from Municipalité Régionale de Comté Le centre de la Mauricie, Québec, Canada in 1996 and 1997. Turtles captured by biased sampling techniques (i.e. at nesting areas) have not been included.

ing several species of plants; leaves and fruits of strawberry plants (*Fragaria* sp.) and birch leaves (*Betula papyrifera*) being commonly eaten. One turtle was observed snipping fern stems at the base and then eating the tip of the frond. Two genera of mushrooms, *Boletus* and *Amanita,* were consumed on several occasions. Invertebrates eaten included slugs, worms and millipedes. Also, turtles were seen fighting over and eating items of carrion, including mice, toads (*Bufo americanus*), and fish. On five occasions, fighting (involving pushing, biting, and hissing) was observed over a piece of carrion; in one instance four turtles were involved. On three separate occasions, turtles were observed with feathers in their mouths.

Mating

Courting and mating activities were observed from May until November. Over the two year study, 35 courting or mating events were observed; 27 (77%) occurred in the fall, 17 (49%) of which occurred in October alone. Mating activities appeared to be more frequent during midday with more than 18 (51.4%) occurring between 11:00 and 13:00. Some females and males engaged in mating activities more than once in a season and with more than one partner. One male was observed coupled with five different females. Turtles were also recorded in mating activities with the same partner during both years of the study.

Injuries, predation, and parasites

Sixty-five (34.6%) turtles had scars from injuries. Of the 188 turtles caught, 46 (28 females, 12 males, and 6 immature) had a part of their tail missing. The proportion of males and females with tail injuries did not differ (χ^2=2.55, P>0.05), but proportionately more adults were injured than immature turtles (χ^2= 7.71, P<0.01). Eighteen (9.6%) turtles had at least partial loss of one limb, with or without a tail injury and 6 (3.2%) had partial loss of two limbs. Differences between sexes (χ^2=0.05, P>0.05) or between adult and immature turtles (χ^2=3.70, P>0.05) for leg damage were not significant. No dead turtles were found during the study. Animals seen in the study area which could have caused these mutilations included Red Fox (*Vulpes fulva*), Muskrat (*Ondatra zibethica*), Otter (*Lontra canadensis*), Striped Skunk (*Mephitis mephitis*), Raccoon (*Procyon lotor*), feral and domestic cats (*Felis domestica*), dogs (*Canis familiaris*) and other Wood Turtles.

Leeches (*Placobdella* sp.) were found attached to many parts of turtles but were most common on the skin of the limb sockets. Leeches were seen on turtles in May (70% of observations), June, September, and October.

TABLE 1. Wood Turtle morphometrics from a population in Municipalité Régionale de Comté Le Centre de la Mauricie, Québec, 1996 - 1997.

Sex	n	Carapace length (mm)	Plastron length (mm)	Mass (g)	Age estimate (annuli count)
Male	55	214.51 ± 4.21*	191.54 ± 11.40	1173 ± 252**	19.7 ± 4.2
Female [a]	83	201.07 ± 10.88	192.69 ± 10.33	1083 ± 168	20.4 ± 4.1
Immature	50	129.56 ± 39.73	122.27 ± 38.74	375 ± 188	7.7 ± 3.9

Note: Values are given as mean ± standard deviation.
[a] all females measured during the study were included
* Significant differences between sexes , t = 1.936, df = 136, P < 0.05.
** Significant differences between sexes , t = 2.49, df = 136, P < 0.01.

Discussion

Population Structure

Our estimate of 238 turtles indicates that Wood Turtles are capable of sustaining a relatively large population at the northern limit of their range. This is the largest known population in the province of Québec. Recruitment appears to be stable, with immature turtles comprising 31% of all turtles captured. Other studies in northern areas have found immature/juvenile turtles to make up much less of the population: 8.5% in Wisconsin (Ross et al. 1991), 12% in the Algonquin Park region, Ontario (Brooks et al. 1992), and 18.8% for the Maitland River in Ontario (Foscarini 1994*). Populations further south seem to have more immature/juvenile turtles: 44% in New Hampshire (Tuttle and Carroll 1997), 46% in West Virginia (Niederberger and Seidel 1999) and 66% in a New Jersey population (Farrell and Graham 1991). The latter study utilized captive turtles to assess reproductive characteristics and it is unclear whether captive hatched individuals were included in the analysis. Spring and fall surveys of our population showed significantly different ratios of adult to immature turtles, with a greater proportion of immature turtles being captured in the fall. This could indicate that there are seasonal differences in behaviour, activities, or habitat use between adult and immature turtles, which may be influencing the proportions captured. Further research into seasonal activity patterns and habitat use are needed for freshwater turtles, the results of which may invalidate attempts to calculate population estimates without taking behaviour into account.

Analysis of recapture data found that juvenile turtles were recaptured at a lower rate than were adult turtles. This would indicate that juvenile turtles comprise even more of the population. However, this result breaks the first assumption of mark-recapture estimates, specifically, that all individuals, including those previously marked have an equal probability of being recaptured. This assumption is rarely if ever met during studies of wild populations of animals (Leslie et al. 1955; Gibbons 1968; Begon 1979; Burnham and Overton 1979). We were able to census a large proportion of the population with relative ease and success and therefore utilized the Lincoln-Peterson method here to get a general estimate of population size (Gibbons 1968; Krebs 1989).

Due to a short growing season, where growth is not interrupted, it was assumed that not more than one growth annulus was deposited per year. Therefore, annuli act as reliable indicators of age, at least until maturity, when growth slows considerably and growth annuli are sometimes too small to distinguish (Harding and Bloomer 1979; Harding 1985*; Lovich et al. 1990). A recent study of Wood Turtles from a population in southern Québec confirmed, based on multiple recaptures, that only one annulus per year is produced (Saumure 1997*). However, we believe that annuli counts are at best minimums because annuli were often too small and/or too worn to count. The validity of using scute annuli to determine age has been questioned for all turtles (Cox et al. 1991; Kennett 1996; Brooks et al. 1997). However, it seems with few exceptions that in temperate climates the counting of scute annuli is a reliable estimator of an individual's age at least to or near the age of maturity (Germano and Bury 1998). Wild Wood Turtles have been known to live as long as 46 years (Ernst 2001b) and captives up to 58 years (Oliver 1955).

In the last ten years, a sufficient number of studies have been published to allow comparisons among populations. Brooks et al. (1992) proposed that average carapace length (CL) from northern Wood Turtle populations are larger and that they mature later and at a larger size than do southern populations. A more recent study (Daigle 1997) confirmed that there was a strong negative correlation between number of FFD and mean size at maturity. However, different researchers take CL measurements with slight variation in the method, some measuring a straight line between the nuchal and supracaudal notches, while others are presenting maximum CL. The differences between methods are minimal and fall well within the standard deviations, thereby allowing valid comparisons of Wood Turtle populations (Table 2). The mean CL for males and females compared (separately) to the number of frost free days (FFD) produces a strong negative correlation (males r=0.845, P<0.001; females r=0.829, P<0.001). The differences between methods in measuring CL may slightly weaken this correlation but the trend would remain. Thus, we conclude that Wood Turtles are larger (CL) as FFD decrease across the species' geographic range.

To test whether turtles were maturing later and at a larger size in northern populations, the number of FFD was compared to minimum CL at maturity and the minimum age at maturity, for males and females separately (Table 2). There was a significant correlation between minimum CL at maturity and FFD (males r=0.734, P<0.05; females r=0.669, P<0.05). This suggests that Wood Turtles are maturing at a larger size in populations with fewer FFDs. There were no significant correlations between FFD and minimum age at maturity. The lack of correlation between these variables could be due to differences in assigning males and females to categories of adult, mature, or sexually mature. The variables that were constant among studies, minimum CL at first nesting (female), and secondary sexual characteristics (male), did show a correlation with FFD. Without standardization of what Wood Turtle traits should be used to assign individuals to specific categories, any relationships among these features will remain unclear.

There appears to be a general trend that male secondary sexual characteristics are apparent at fewer annuli than sexual maturity for females (Table 2). In

TABLE 2. Comparisons of frost-free days with carapace length, age, minimum age, and size at maturity of adult Wood Turtles among 11 locations.

		MALES				FEMALES				
			Carapace length Mean	Number of annuli			Carapace length Mean	Number of annuli		
Location	FFD[a]	n	(range)	Mean	Min.	n	(range)	Mean	Min.	Source
ON (45 °N)	90	21	219 (199-244)	21.6	17	57	202 (185-225)	24.6	18	Brooks et al. 1992
QC (46°N)	100	55	215 (170-242)	19.7	11	83	201 (181-225)	20.4	14	Present study
QC (45.5°N)	113	9	216 (176-238)	16.8	10	10	201 (195-?)	16.8	15	Saumure and Bider 1998; Saumure 1992
QC (45°N)	120	19	195 (176-211)	—	—	23	182 (167-209)	—	—	Daigle 1997
WS (44°N)	140	28	201 (—)	—	—	48	187 (—)	—	—	Ross et al. 1991
MI (46°N)	140	86	200 (169-228)	21.5	12	10	182 (158-218)	20.2	15	Harding and Bloomer 1979
ON (43°N)	150	83	198 (173-?)	21.1	12	13	181 (158-?)	20.5	10	Foscarini 1994*
NH (43°N)	150	17	182 (—)	—	—	29	172 (—)	—	—	Tuttle and Carroll 1997
VA (39°N)	190	11	196 (—)	—	5	14	183 (—)	—	—	Lovich et al. 1990
NJ (41°N)	210	311	178 (160-206)	—	7-8	464	165 (160-188)	—	7-8	Harding and Bloomer 1979
NJ (41°N)	210	69	177 (161-201)	—	14	49	171 (158-200)	—	14	Farrell and Graham 1991

ON-Ontario, QC-Quebec, WS-Wisconsin, MI-Michigan, NH-New Hampshire, VA-Virginia, NJ-New Jersey
Note: Approximate latitudes are estimated from locations provided in the sources.
[a] Mean number frost-free days (U.S. Department of Commerce, Environmental Data Service (1968) and Wilson (1971)).

this study we found males to have secondary sexual characteristics at 11 annuli, while females weren't assigned a sex until 14 annuli. This may be attributed to the fact that the only way to confirm a turtle is female is to observe her to be gravid or nesting, whereas a male can be distinguished by secondary sexual characteristics. It is possible that these characteristics begin to be displayed prior to sexual maturity thus biasing samples by inclusion of immature males. In our study, the youngest male observed attempting to copulate was 15, while the youngest showing secondary sexual characteristics was 11 and the youngest female observed nesting was 14. Because most mating occurs in the fall (after the year's growth) and nesting occurs in the spring (before the year's growth) it is apparent that both females and males in our northern population are sexually mature at a minimum of 15 years. Differences reported in other studies may result from comparing puberty for males with sexual maturity for females.

Differing growth rates among individuals complicate the use of a minimum age at which sexual status is assigned, because all turtles are not necessarily sexually mature at the same age. The range of CL for all turtles with 15 annuli was 170 – 242 mm, a difference of 72 mm. The small turtle (CL = 170 mm) was recorded as immature and the large turtle (CL = 242 mm) was distinctly male (Figure 1). Due to the large differences in size at a given age, we used a minimum size based on CL to assign sexual status. For many species of turtles, it has been found that size, not age, influences attainment of maturity (Cagle 1948; Gibbons 1968; Congdon et al. 1983; Ross 1989) and for other species it is age (Tinkle 1961; Graham and Doyle 1977). Table 2 illustrates that while the minimum age at which maturity was assigned

varied greatly among populations, the general size (CL) at sexual maturity appears to be similar for most studies, approximately 160 to 180 mm. There is, however, a correlation towards a larger minimum size at maturity at more northerly locations. A larger body size may be necessary at northern locations for sufficient reserves to be accumulated so an individual can survive hibernation and reproduce without threatening their well-being (Galbraith et al. 1989; Miller and Hickling 1990; Brooks et al. 1992; Saumure and Bider 1998).

Sex and immature : adult ratios

Sex ratios for other Wood Turtle populations have ranged from 1 : 1.9 to 1 : 0.8, males to females respectively (Farrell and Graham 1991; Ross et al. 1991). Because Wood Turtles do not show temperature dependent sex determination (Bull et al. 1985), no sexual biases are expected. Our study found that the sex ratio did not differ significantly from 1 : 1, which is similar to most other studies (Harding and Bloomer (Michigan) 1979; Harding 1985*; Farrell and Graham 1991; Ross et al. (BR site) 1991; Kaufmann 1992; Daigle 1997; Tuttle and Carroll 1997; Saumure 1997*). The few studies that show ratios significantly different from 1 : 1 (Harding and Bloomer (New Jersey) 1979; Ross et al. (WR) 1991; Foscarini 1994*) may result from either biased sampling (as was observed in our study when several females were captured at a communal nesting area, the removal of which gave a 1:1 ratio), factors that may be unequally removing one sex from the population (e.g., females being killed on roads while searching for a nest site), the use of inappropriate size/age classes to distinguish males from females (as immature turtles often resemble females), or a combination of the above (Ream and Ream 1966; Gibbons 1970; Stickel 1978; Harding and Bloomer 1979; Litzgus and Brooks 1996*).

Dietary Habits

Observations of feeding habits support the claim that Wood Turtles are opportunistic omnivores (Harding and Bloomer 1979). Three feeding observations were of particular interest. A turtle cut down large fern fronds by biting through the stem and then ate only the fresh growing tips. This illustrates a complex feeding strategy that must be learned and remembered, only being applicable during a short period of the year and may indicate a degree of intelligence, previously noted for this species (Tinkelplaugh 1932). Wood Turtles may also be opportunistically carnivorous. Surface (1908) examined stomach contents of Wood Turtles and found bird remains in 8% of samples and Harding and Bloomer (1979) document the eating of eggs or young birds. Observations in our study also indicated the consumption of bird parts, either captured alive or scavenged as carrion; a similar observation was made by Niederberger and Seidel (1999). We observed turtles eating fish, bird, toad and mouse carrion. Feeding on carrion of fish and birds has also been documented by Surface (1908), Harding and Bloomer (1979), and Farrell and Graham (1991). Harding and Bloomer (1979) also document the eating of newborn mice. In captivity, Wood Turtles eat many meaty items (Harding and Bloomer 1979; Merrit 1980). Some populations have been reported to have developed an apparently successful strategy to obtain animal protein, known as "stomping", used to lure earthworms to the surface (Kaufmann 1986; Kaufmann et al. 1989). Wood Turtles did consume earthworms during the present study but this feeding strategy was not observed.

Because Wood Turtles at the northern limit of their range are larger than those from the south and their annual period of activity is shorter, northern turtles may need to consume more protein. During our study, up to four turtles were observed fighting over a piece of carrion, suggesting that meat is a favoured food. It has been suggested that growth in some turtles is limited by the relative amount of protein in their diet (Gibbons 1967; Zug 1993) and that larger body sizes can result from increased carnivory (MacCulloch and Secoy 1983).

Mating

Most of our observations of courting behaviour were in spring and fall when turtles were congregated in aquatic habitats, confirming the bimodal pattern observed by others (Carroll and Ehrenfeld 1978; Harding and Bloomer 1979; Farrell and Graham 1991; Kaufmann 1992; Foscarini 1994*). Although mating activities can occur during any month that turtles are active, it is more frequently observed in spring and fall. This may be the result of hormonal fluctuations (Licht 1982) and/or simply because males and females are congregated in aquatic habitats during these periods (Harding and Bloomer 1979). In an Ontario population, 50% of courting behaviour observed was during May and there was at least one observation per month from June to September, but very little observation was conducted during September and October (Foscarini 1994*). The frequency of fall mating may have been overlooked in that study (telemetry surveys were conducted every three to four weeks) (Foscarini 1994*). In our study, 50% of the courting activities were observed during October alone, and 70% occurred during the fall. If anything, this was an underestimate of the importance of the fall mating period, as we also spent less time in the field during the autumn months. Similar results showing an increase in mating behaviour in the fall were reported by Harding (1990). Carroll and Ehrenfeld (1978) observed that mating behaviours peaked in the spring, with a second mating period occurring in September and October. They also reported that fall mating attempts were longer than those in the spring. Further support of the importance of the fall mating period is provided by Kaufmann (1992), who also found that fall mountings were of a longer duration than spring mountings and that significantly

more fall mating attempts resulted in insemination. The suggestion that the increase in mating behaviour in fall was a result of hormonal fluctuations was confirmed by Licht (1982) who reported that testosterone production and spermatogenesis peak during late summer and fall. In Nova Scotia, Powell (1967) found that female turtles in summer and fall have mature follicles, which are then stored over winter, and ovulated in the spring. If the fall is, in fact, the primary mating period for this species, females must be capable of storing sperm to fertilize eggs the following spring, as has been suggested by another study (Kaufmann 1992). The storage of viable sperm for over one year has been documented for many other species of North American turtles (Smith 1956; Berry and Shine 1980; Gist and Jones 1989), but has not been shown for Wood Turtles. While we have no evidence that our population has longer mating attempts in the fall or that there is a greater frequency of sperm transfer during this period, the fact that 70% of mating attempts observed occurred in the fall may indicate that the fall mating period is more important. At our northern location there is little post-hibernation time (2-3 weeks) in the spring before it is necessary for female turtles to ovulate their mature follicles, in preparation for oviposition by mid-June. If the spring was the period that was important for mating activities, we should have observed numerous matings in the spring, but did not. Disturbances to Wood Turtle populations during the fall may disrupt mating activities and have a negative effect on reproductive output.

Our observations that mating occurred most often between 11:00 and 13:00 differ from those reported in other studies. Farrell and Graham (1991) report that mating was commonly observed in the early morning, while others (Harding and Bloomer 1979) report that it is most often observed in late afternoon. It is possible that our population was mating during the midday period because this is the time at which the turtle has had sufficient time to emerge from the water and bask to increase its body temperature. Turtles are typically temperature sensitive related to their activity and turtles that are larger, as our study population was, may require more basking time to reach temperatures that are ideal for normal activity (Boyer 1965; Cloudsey-Thompson 1971; Hutchison 1979; Huey 1982). In a controlled experiment, Wood Turtles maintained at a higher temperature had several activity periods during the day, while those kept at a lower temperature had only one activity period centered around midday (Graham and Dadah-Tosti 1981). Our observations of mating behaviour centered around midday may be explained by these results. This could also explain why mating behaviour in southern populations occurs during the early morning and evening, times at which turtles were more active (Harding and Bloomer 1979; Farrell and Graham 1991).

Injuries, Predation, and Parasites

Commonly reported injuries to Wood Turtles include tail loss, partial or complete amputation of limb(s) and shell damage (Farrell and Graham 1991; Brooks et al. 1992; Kaufmann 1992; Foscarini 1994*; Gilhen et al. 1994*; Saumure and Bider 1998) all of which may eventually lead to premature death. Partial tail loss was the most common reported injury and the rate of loss, 24.5% in our study, is within the range of other studies, 59% in Ontario (Foscarini 1994*) to 16.8% in New Jersey (Farrell and Graham 1991). As in Saumure and Bider (1998), there was no difference for the rates of partial tail amputation between sexes in adults; however, loss was less in immature turtles. This may simply be an artifact of adult turtles having lived longer. It is also possible that immature turtles, because their shell is not completely ossified (Zug 1991) are more often killed outright (Wilbur 1975; Bury 1979). However, tail damage may not be solely the result of predation but may also be inflicted during aggressive adult turtle encounters for dominance and mate selection. Tail injuries are known to be caused by conspecifics in captivity (Bell 1972). During this study, aggressive encounters in which tail biting occurred were observed between males and males, females and males (precopulatory), and females and females. Prolonged tail biting by turtles of the genera *Clemmys* and *Glyptemys* is known to occur during agonistic encounters is considered to be a highly aggressive act (Ernst 1967; Kaufmann 1992), but it is not clear if any permanent damage is incurred. During this study, bleeding was observed on two occasions after a tail had been bitten, once in a male-male encounter and the other in a female-female. ADW, having being bitten on a finger by a female Wood Turtle has experienced the strength of a Wood Turtle's bite, which removed a large chunk of skin and left a deep wound. It is possible that such an attack to a tail could sever the caudal veins, causing part of the tail to atrophy.

The results obtained for limb amputation (9.6%) are similar to those obtained by others: 9.6%, Harding and Bloomer (1979); 8.6%, Farrell and Graham (1991); 12.9%, Foscarini (1994*). The percentage having two limbs partially amputated (3.2%) is similar to that reported by Harding and Bloomer (1979). Several studies report that it is not uncommon to find turtles with one or two limbs chewed off by a predator such as a raccoon (Harding and Bloomer 1979; Harding 1985; Farrell and Graham 1991) or otter (Gilhen et al. 1994*), but in the latter study it is not clear whether they observed this mutilation directly. A study in southern Québec (Saumure and Bider 1998) reported a much higher rate of limb amputation, 32.3%, and a double amputation rate of 13%. Saumure and Bider (1998) suggested that a few very efficient predators or the relative abundance/density of the predatory species could explain the high rates of limb amputation. The

effects of limb amputations on turtles are unknown. However, Harding (1985) did notice there were significantly fewer injured turtles recaptured during his study, suggesting that long-term survival may be compromised.

The seasonal occurrence of leeches on Wood Turtles has been well documented (Koffler et al. 1978; Harding and Bloomer 1979; Farrell and Graham 1991; Foscarini 1994*; Saumure and Bider 1996). We found no turtles with leeches during summer months and believe that this is because Wood Turtles are primarily terrestrial at this time, as has been suggested by others. While some studies report leeches on Wood Turtles in all months (Harding and Bloomer (Michigan) 1979; Foscarini 1994*), each presence is highest in the spring. These latter observations are from populations in the western part of the species' range; these populations are thought to be more aquatic than eastern populations (Harding and Bloomer 1979).

Population Density

The density of Wood Turtles in our study area was approximately 0.44 turtles per hectare (tu/ha). This density is slightly higher than that for turtles from a population in central Ontario, 0.24 tu/ha (Brooks et al. 1992), a site where the number of frost-free days (FFD) is lower than ours (Table 3). Densities of Wood Turtles from southern locations with more FFD are greater, for example, 2.6 tu/ha for a New Hampshire population (Tuttle and Carroll 1997) and 10.7 tu/ha for a population in New Jersey (Farrell and Graham 1991). The density of turtles is strongly positively correlated with the number of FFD (r=0.947, P<0.01). It is possible that because northern turtles are larger they require a greater area in which to forage to obtain the necessary resources and build sufficient fat reserves to survive the longer winters. Arvisais et al. (2002) noted that there was a trend towards larger home ranges in northern populations. It could also be that the general trend of decreasing biodiversity and primary productivity associated with shorter growing seasons may be limiting the numbers and/or the variety of food available to northern turtles (Fleming 1973; Heywood 1978; Currie and Paquin 1987; Cox and Moore 1995). This could be forcing turtles to utilize a larger area so dietary requirements can be met. Food availability has been suspected of limiting the density of other turtles (Ross 1989) and may help explain the aggressive encounters we observed over food.

Acknowledgments

This study was part of a larger program initiated by Société de la faune et des parcs du Québec, Direction de la faune et des habitats, Parks Canada, St. Lawrence Valley Natural History Society, McGill University, and l'Université du Québec à Trois-Rivières. Funding, equipment, and personnel for this research were generously provided to the St. Lawrence Valley Natural History Society by Parks Canada, Fondation de la Faune du Québec, and Société de la faune et des parcs du Québec. We thank all those who aided this project by assisting with the field work. Earlier drafts of the manuscript were improved by discussions with and/or reviews by Francis Cook, R. K. Stewart, Marcella Trembley, David Rodrigue, Raymond Saumure, and two anonymous reviewers. This paper was submitted in partial fulfillment of the requirements for the degree of Master of Science to the Department of Natural Resource Sciences of McGill University.

Documents Cited (marked with * after date in text)

Allard, M. 1978. Parc national de la Mauricie, étude géomormophologie. Rapport final préparé pour Parcs Canada. Laboratoire de Géomorphologie, Département de géographie, Université Laval, Québec. 155 pages.

Foscarini, D. A. 1994. Demography of the Wood Turtle (*Clemmys insculpta*) and habitat selection in the Maitland River Valley. M.Sc. thesis, University of Guelph, Ontario. 108 pages.

Gilhen, J., T. Herman, and **N. Meister.** 1994. The Wood Turtle: an uncertain future in Nova Scotia. Turtle Watch, Centre for Wildlife and Conservation Biology. Acadia University, Nova Scotia. Unpublished. 5 pages.

Harding, J. H. 1985. Comments on age determination and growth in the Michigan population of the Wood Turtle (*Clemmys insculpta*). Combined meeting of SSAR and HL. University of South Florida, Tampa. Page 149. (Abstract)

Harding, J. H. 1991. Communications. *Clemmys* Interest Group Newsletter (May). 4 pages.

TABLE 3. Comparison of frost-free days and Wood Turtle density (number of turtles/hectare) among six locations.

	FFD[a]	turtles/hectare	Source
Ontario (45°N)	90	0.24	Brooks et al. 1992
Québec (46°N)	100	0.44	Present study
Michigan (46°N)	140	2.5	Harding and Bloomer 1979
New Hampshire (43°N)	150	2.6	Tuttle and Carroll 1997
New Jersey (41°N)	210	10.7	Farrell and Graham 1991
New Jersey (41°N)	210	12.5	Harding and Bloomer 1979

Note: Approximate latitudes are estimated from locations provided in the sources.

[a] Mean number frost-free days (U.S. Department of Commerce, Environmental Data Service (1968) and Wilson (1971)).

Klemens, M. W. 1992. Proposal to amend C.I.T.E.S. Appendix II. with addition of: Wood Turtle *Clemmys insculpta* (Le Conte). Unpublished. 7 pages.

Litzgus, J. D., and **R. J. Brooks.** 1996. Status of the Wood Turtle, *Clemmys insculpta*, in Canada. COSEWIC report, draft copy 14 February, 1996. Unpublished. 70 pages.

Saumure, R. A. 1995. Turtle research in the Big Creek National Wildlife Area. Report to Canadian Wildlife Service. London, Ontario. 81 pages.

Saumure, R. A. 1997. Growth, mutilation, and age structure of two populations of Wood Turtles (*Clemmys insculpta*) in southern Québec. M.Sc. thesis, McGill University, Québec. Unpublished. 70 pages.

Literature Cited

Arvisais, M., J.-C. Bourgeois, E. Levesque, C. Daigle, D. Masse, and **J. Jutras.** 2002. Home range and movements of a Wood Turtle (*Clemmys insculpta*) population at the northern limit of its range. Canadian Journal of Zoology 80: 402-408

Beaulieu, H. 1992. Liste de la faune vertébrée susceptible d'être désignée menacée ou vulnérable. Québec, Ministère du Loisir, de la Chasse et de la Pêche.

Begon, M. 1979. Investigating animal abundance: capture-recapture for biologists. Edward Arnold Limited, London.

Bell, V. 1972. Turtle of the month. New York Turtle and Tortoise Society 1: 5-7.

Berry, J. F., and **R. Shine.** 1980. Sexual size dimorphism and sexual selection in turtles (order Testudines). Oecologia 44: 185-191.

Bider, J. R., and **S. Matte.** 1996. An atlas of reptiles and amphibians of Québec. St. Lawrence Valley Natural History Society and Ministère de l'Environnement et de la Faune, Québec.

Boyer, D. R. 1965. Ecology of the basking habit in turtles. Ecology 46: 99-118.

Brewster, K. N., and **C. M. Brewster.** 1991. Movement and microhabitat use by juvenile Wood Turtles introduced into a riparian habitat. Journal of Herpetology 25: 379-382.

Brooks, R. J., C. M. Shilton, G. P. Brown, and **N. W. S. Quinn.** 1992. Body size, age distribution, and reproduction in a northern population of Wood Turtles (*Clemmys insculpta*). Canadian Journal of Zoology 70: 462-469.

Brooks, R. J., M. A. Krawchuk, C. Stevens, and **N. Koper.** 1997. Testing the precision and accuracy of age estimation using lines in scutes of *Chelydra serpentina* and *Chrysemys picta*. Journal of Herpetology 31: 521-529.

Buhlmann, K. 1992. Legislation & conservation alert. Herpetological Review 23: 66.

Buhlmann, K. A. 1993. Legislation & conservation alert. Herpetological Review 24: 125.

Bull, J. J., J. M. Legler, and **R. C. Vogt.** 1985. Non-temperature dependent sex determination in two suborders of turtles. Copeia 1985: 784-786.

Burnham, K. P., and **W. S. Overton.** 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology 60: 927-936.

Bury, R. B. 1979. Population ecology of freshwater turtles. Pages 571-602 *in* Turtles: Perspectives and Research. *Edited by* M. Harless and H. Morlock. John Wiley and Sons Publishing, New York.

Cagle, F. R. 1939. A system for marking turtles for future identification. Copeia 1939: 170-173.

Cagle, F. R. Î948. Sexual maturity in the male turtle, *Pseudemys scripta troostii*. Copeia 1948: 108-111.

Carroll, T. E., and **D. W. Ehrenfeld.** 1978. Intermediate-range homing in the Wood Turtle. Copeia 1978: 117-126.

Cloudsey-Thompson, J. L. 1971. The temperature and water relation in reptiles. Merrow Publication Co. Ltd. Watford Herts, England.

Congdon, J. D., D. W. Tinkle, G. L. Breitenbach, and **R. van Loben Sels.** 1983. Nesting ecology and hatching success in the turtle *Emydoidea blandingi*. Herpetologica 39: 417-429.

Cox, C. B., and **P. D. Moore.** 1995. Biogeography: An ecological and evolutionary approach. Blackwell Science Ltd. Cambridge, Massachusetts.

Cox, W. A., J. B. Hazelrig, M. E. Turner, R. A. Angus, and **K. R. Marion.** 1991. A model for growth in the Musk Turtle, *Sternotherus minor*, in a north Florida spring. Copeia 1991: 954-968.

Currie, D. J., and **V. Paquin.** 1987. Large-scale biogeographical patterns of species richness of trees. Nature 329: 326-327.

Daigle, C. 1997. Size and characteristics of a Wood Turtle, *Clemmys insculpta*, population in southern Québec. Canadian Field-Naturalist 111: 440-444.

Ernst, C. H. 1967. A mating aggregation of the turtle *Clemmys guttata*. Copeia 1967: 473-474.

Ernst, C. H. 1986. Environmental temperatures and activities in the Wood Turtle, *Clemmys insculpta*. Journal of Herpetology 20: 222-229.

Ernst, C. H. 2001a. An overview of the North American turtle genus *Clemmys* Ritgen, 1828. Chelonian Conservation and Biology 4: 211-216.

Ernst, C. H. 2001b. Some ecological parameters of the Wood Turtle, *Clemmys insculpta*, in southeastern Pennsylvania. Chelonian Conservation and Biology 4: 94-99.

Ernst, C. H., J. E. Lovich, and **R. W. Barbour.** 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington.

Farrar, J. L. 1995. Trees in Canada. Fitzhenry and Whiteside Limited, Ontario.

Farrell, R. F., and **T. E. Graham.** 1991. Ecological notes on the turtle *Clemmys insculpta* in Northwestern New Jersey. Journal of Herpetology 25: 1-9.

Fleming, T. H. 1973. Numbers of mammal species in North and Central American forest communities. Ecology 54: 555-563.

Froese, A. D., and **G. M. Burghardt.** 1975. A dense natural population of the common Snapping Turtle (*Chelydra s. serpentina*). Herpetologica 31: 204-208.

Galbraith, D. A., R. J. Brooks, and **M. E. Obbard.** 1989. The influence of growth rate on age and body size at maturity in female Snapping Turtles (*Chelydra serpentina*). Copeia 1989: 896-904.

Galois, P., and **J. Bonin.** 1999. Rapport sur la situation de la Tortue des Bois (*Clemmys insculpta*) au Québec. Faune et Parcs Québec, Direction de la faune et des habitats, Québec.

Garber, S. D. 1989. Population ecology of the Wood Turtle (*Clemmys insculpta*). Pages 31-35 *in* Proceedings, 12th International Herpetological Symposium. *Edited by* M. J. Rosenberg. Thurmont, Maryland.

Garber, S. D., and **J. Burger.** 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. Ecological Applications 5: 1151-1162.

Germano, D. J., and **R. B. Bury.** 1998. Age determination in turtles: Evidence of annual deposition of scute rings. Chelonian Conservation and Biology 3: 123-132.

Gibbons, J. W. 1967. Variation in growth rates in three populations of the Painted Turtle, *Chrysemys picta*. Herpetologica 23: 296-303.

Gibbons, J. W. 1968. Population structure and survivorship in the Painted Turtle (*Chrysemys picta*). Copeia 1968: 260-268.

Gibbons, J. W. 1970. Sex ratios in turtles. Researches on Population Ecology 12: 252-254.

Gist, D. H., and **J. M. Jones.** 1989. Sperm storage within the oviduct of turtles. Journal of Morphology 199: 379-384.

Graham, T. E., and **S. D. Doyle.** 1977. Growth and population characteristics of Blanding's Turtle, *Emydoidea blandingii*, in Massachusetts. Herpetologica 33: 410-414.

Graham, T. E., and **J. Dadah-Tosti.** 1981. Temperature effects on locomotor patterns in the Wood Turtle, *Clemmys insculpta*. Bulletin of the Maryland Herpetological Society 17: 74-77.

Green, D. M. 1996. COSEWIC designates the Wood Turtle a vulnerable species. Canadian Association of Herpetologists, Bulletin. 10: 9.

Harding, J. H. 1985. *Clemmys insculpta*. Predation-mutilation. Herpetological Review 16: 30.

Harding, J. H. 1990. A twenty year Wood Turtle study in Michigan: implication for conservation. Pages 31-35 *in* Proceedings of the First International Symposium on turtles and tortoises: conservation and captive husbandry. *Edited by* K. R. Beamen, R. Kent, F. Caporaso, S. McKeown, and M. D. Graff. California Turtle and Tortoise Club.

Harding, J. H., and **T. J. Bloomer.** 1979. The Wood Turtle, *Clemmys insculpta* ... a natural history. (Herp) Bulletin of the New York Herpetological Society 15: 9-26.

Heywood, V. H. *Editor.* 1978. Flowering plants of the world. Oxford University Press, Oxford.

Huey, R. B. 1982. Temperature, physiology and the ecology of reptiles. Pages 25-91 *in* Biology of the Reptilia, Volume 12 Physiology (C): Physiological Ecology. *Edited by* C. Gans and F. H. Pough. Academic Press, London, England.

Hutchison, V. H. 1979. Thermoregulation. Pages 207-228 *in* Turtles: Perpectives and Research. *Edited by* M. Harless and H. Morlock. J. Wiley and Sons, New York.

Kaufmann, J. H. 1986. Stomping for earthworms by Wood Turtles, *Clemmys insculpta*: a newly discovered foraging technique. Copeia 1986: 1001-1004.

Kaufmann, J. H. 1992. The social behaviour of Wood Turtles (*Clemmys insculpta*) in Central Pennsylvania. Herpetological Monographs 6: 1-25.

Kaufmann, J. H. 1995. Home ranges and movements of Wood Turtles, *Clemmys insculpta*, in central Pennsylvania. Copeia 1995: 22-27.

Kaufmann, J. H., J. H. Harding, and **K. N. Brewster.** 1989. Worm stomping by Wood Turtles revisited. Bulletin of the Chicago Herpetological Society 24: 125-126.

Kennett, R. 1996. Growth models for two species of freshwater turtle, *Chelodina rugosa* and *Elseya dentata*, from the wet-dry tropics of northern Australia. Herpetologica 52: 383-395.

Koffler, B. R., R. A. Seigel, and **M. T. Mendonca.** 1978. The seasonal occurrence of leeches on the Wood Turtle, *Clemmys insculpta*, (Reptilia, Testudines, Emydidae). Journal of Herpetology 12: 571-572.

Krebs, C. J. 1989. Ecological methodology. Harper Collins, New York.

Leslie, P. H., D. Chitty, and **H. Chitty.** 1955. The estimation of population parameters from data obtained by means of capture-recapture method. III. An example of the practical applications of the method. Biometrika 40: 137-169.

Levell, J. P. 2000. Commercial exploitation of Blanding's Turtle, *Emydoidea blandingii*, and the Wood Turtle, *Clemmys insculpta*, for the live animal trade. Chelonian Conservation and Biology 3: 665-674

Lindeman, P. V. 1990. Closed and open model estimates of abundance and tests of model assumptions for two population of the turtle, *Chrysemys picta*. Journal of Herpetology 24: 78-81.

Licht, P. 1982. Endocrine patterns in the reproductive cycle of turtles. Herpetologica 38: 51-61.

Lovich, J. E., C. H. Ernst, and **J. F. McBreen.** 1990. Growth, maturity, and sexual dimorphism in the Wood Turtle, *Clemmys insculpta*. Canadian Journal of Zoology 68: 672-677.

MacCulloch, R. D., and **D. M. Secoy.** 1983. Demography, growth, and food of Western Painted Turtles, *Chrysemys picta belli* (Gray), from southern Saskatchewan. Canadian Journal of Zoology 61: 1499-1509.

Merrit, D. A. 1980. The Wood Turtle, *Clemmys insculpta*. Natural history, behaviour, and food habits. Bulletin of the Chicago Herpetological Society 15: 6-9.

Miller, J. S., and **G. J. Hickling.** 1990. Fasting endurance and the evolution of mammalian body size. Functional Ecology 4: 5-12.

Niederberger, A. J., and **M. E. Seidel.** 1999. Ecology and status of a Wood Turtle (*Clemmys insculpta*) population in West Virginia. Chelonian Conservation and Biology 3: 414-418.

Oliver, J. A. 1955. The natural history of North American amphibians and reptiles. Van Nostrand, Princeton.

Pollock, K. H., J. D. Nichols, C. Brownie, and **J. E. Hines.** 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107: 1-97.

Powell, C. B. 1967. Female sexual cycles of *Chrysemys picta* and *Clemmys insculpta* in Nova Scotia. Canadian Field-Naturalist 81: 134-140.

Quinn, N. W. S., and **D. P. Tate.** 1991. Seasonal movements and habitat of Wood Turtles (*Clemmys insculpta*) in Algonquin Park, Canada. Journal of Herpetology 25: 217-220.

Ream, C., and **R. Ream.** 1966. The influence of sampling methods on the estimation of population structure in Painted Turtles. American Midland Naturalist 75: 325-338.

Ross, D. A. 1989. Population ecology of Painted and Blanding's turtles (*Chrysemys picta* and *Emydoidea blandingi*) in Central Wisconsin. Wisconsin Academy of Science, Arts, and Letters 77: 77-84.

Ross, D. A., K. N. Brewster, R. K. Anderson, N. Ratner, and **C. M. Brewster.** 1991. Aspects of the ecology of Wood Turtles, *Clemmys insculpta*, in Wisconsin. Canadian Field-Naturalist 105: 363-367.

Saumure, R. A. 1992. *Clemmys insculpta* (Wood Turtle). Size. Herpetological Review 23:116.

Saumure, R. A., and **J. R. Bider.** 1996. *Clemmys insculpta* (Wood Turtle). Ectoparasites. Herpetological Review 27: 197-198.

Saumure, R. A., and **J. R. Bider.** 1998. Impact of agricultural development on a population of Wood Turtles (*Clemmys insculpta*) in Southern Québec, Canada. Chelonian Conservation and Biology 3: 37-45.

Smith, H. M. 1956. Handbook of amphibians and reptiles of Kansas. University of Kansas Museum of Natural History Miscellaneous Publications 9: 1-356.

SPSS Inc. 2002. SigmaPlot 8.02 user's guide. SPSS Inc. Chicago, Illinois.

Stickel, L. F. 1978. Changes in a Box Turtle population during three decades. Copeia 1978: 221-225.

Surface, H. A. 1908. First report on the economic features of the turtles of Pennsylvania. Zoological Bulletin, Division of Zoology, Pennsylvania Department of Agriculture 6: 105-196.

Tinkelplaugh, O. 1932. Maze learning of a turtle. Journal of Comparative Psychology 13: 201-206.

Tinkle, D. W. 1961. Geographic variation in reproduction, size, sex ratio and maturity of *Sternothaerus odoratus* (Testudinata: Chelydridae). Ecology 42: 68-76.

Tuttle, S. A., and **D. M. Carroll.** 1997. Ecology and natural history of the Wood Turtle (*Clemmys insculpta*) in south New Hampshire. Linnaeus Fund Research Report. Chelonian Conservation and Biology 2: 447-449.

United States Environmental Data Service. 1968. Climatic atlas of the United States. Environmental Data Service, Washington, D.C.

Wilbur, H. M. 1975. The evolutionary and mathematical demography of the turtle *Chrysemys picta*. Ecology 56: 64-77.

Wilson, C. V. 1971. The climate of Québec. Part One. Climatic Atlas. Canadian Meteorological Service.

Wright, A. H. 1918. Notes on *Clemmys*. Proceedings of the Biological Society of Washington 31: 51-58.

Zug, G. R. 1991. Age determination in turtles. Society for the Study of Amphibians and Reptiles, Herpetological Circular 20. 28 pages.

Zug, G. R. 1993. Herpetology. An introductory biology of amphibians and reptiles. Academic Press Incorporated, New York.

Received 2 April 2001
Accepted 12 November 2003

Small Mammal Abundance and Diversity in Forests With and Without Canada Yew, *Taxus canadensis*

JERROLD L. BELANT[1] and STEVE K. WINDELS[2]

[1]National Park Service, Pictured Rocks Science Center, Box 40, Munising, Michigan 49862 USA
[2]Michigan Technological University, School of Forestry and Wood Products, 1400 Townsend Drive, Houghton, Michigan 49849 USA

Belant, Jerrold L, and Steve K. Windels. 2003. Small mammal abundance and diversity in forests with and without Canada Yew, *Taxus canadensis*. Canadian Field-Naturalist 117(3): 389–392.

Canada Yew (*Taxus canadensis*) has been extirpated from much of its former range in northeastern North America possibly due to logging, fire, agriculture, and browsing by White-tailed Deer (*Odocoileus virginianus*). We compared the relative abundance and species diversity of small mammals in five northern hardwood stands containing Canada Yew to five adjacent stands without Canada Yew in the Upper Peninsula of Michigan, during October-November 2000. Overall, 72 individuals were captured (53 in yew, 19 in non-yew); dominant species were Short-tailed Shrew (*Blarina brevicauda*), Deer Mouse (*Peromyscus maniculatus*), and Red-backed Vole (*Clethrionomys gapperi*). Overall mean (± sd) capture rate (individuals/100 adjusted trap nights) in sites with yew (5.5 ± 2.2) was greater ($P = 0.04$) than mean capture rate in sites without yew (1.9 ± 1.0). Three indices of species diversity suggested greater small mammal diversity in stands with Canada Yew understories in northern hardwood forests.

Key Words: Canada Yew, *Taxus canadensis*,.diversity, Michigan, relative abundance, small mammals.

Canada Yew (*Taxus canadensis*) is an evergreen shrub native to the mixed conifer-hardwood forest of northeastern North America (Martell 1974). Canada Yew requires shaded and moist habitats (Stachowicz and Allison 1995), and is intolerant of even moderate herbivory (Leopold et al. 1947; Snyder and Janke 1976; Allison 1990) and disturbance (e.g., clearcutting; Beals and Cottam 1960; Stachowicz and Allison 1995). Canada Yew has been extirpated from much of its former range in the United States as a consequence of logging and subsequent fire, clearing of land for agriculture, and increased browsing by White-tailed Deer (*Odocoileus virginianus*) due to population irruptions (Allison 1990; Stachowicz and Allison 1995).

Little information is available regarding the relationship between Canada Yew and bird and small mammal communities. Because of its former range extent and probable importance to forest structure, loss of Canada Yew may have resulted in changes in vertebrate community structure. For example, Black-throated Blue Warblers (*Dendroica caerulescens*) frequently nest in Canada Yew when it is available (Bent 1963; Holmes 1994). In addition, Canada Yew arils (fruit) and seeds are reportedly eaten by several species of rodents and birds (Fordham 1967 in Martell 1974; Wilson et al. 1996). The structure of Canada Yew may also provide vertical foraging substrate and cover for several rodent species (Kurta 1995). However, we are unaware of other studies describing the importance of Canada Yew to small mammal communities. Our objective was to compare the relative abundance and diversity of small mammals in northern hardwood forests, with and without a Canada Yew understory.

Study Area

The study was conducted in the northcentral Upper Peninsula of Michigan on lands administered by Pictured Rocks National Lakeshore and Shelter Bay Forests, Incorporated (46°27'N, 86°33'W). Total mean annual precipitation was 86 cm, including mean annual snowfall of about 380 cm (Danz 1998). Temperatures during the study ranged from about –2 to 21°C. Much of the study area was clearcut in the early 1900s (Frederick et al. 1977), but stands have regenerated to Sugar Maple (*Acer saccharum*) and American Beech (*Fagus grandifolia*), which comprised 90% of the trees in the area (Danz 1998). Canada Yew has been present in the study area for ≥50 years (Danz 1998); mean maximum height of Canada Yew on study sites was about 1 m.

Methods

Field work was conducted from 31 October to 13 November 2000. Five locations were selected. Each location consisted of a treatment (stand with yew understory) and control (stand without yew understory) site, with paired sites separated by 25-100 m. Yew sites varied from about 0.3-7.0 ha. Twenty-five stations were located at 10 m intervals in 3-4 lines separated by 10 m. Number of lines and number of stations/line were adapted to individual yew stands. Stations in sites with yew were ≥5 m from the edge of yew cover. Two Victor® mouse snap traps (Woodstream Corporation, Lititz, Pennsylvania, USA) were positioned at each station and baited with a mixture of peanut butter and rolled oats. At each station, traps were separated by ≥1 m and were ≤1.5 m from survey flags. Traps were checked daily and removed after 4 days of trapping

effort. Thus, each site received 200 unadjusted trap nights of effort. Traps that were sprung with or without capture were adjusted as representing 0.5 trap nights (Belant 1992; Beauvais and Buskirk 1999). All small mammals captured were removed from traps and weighed; traps were rebaited as necessary.

At each trap station, we visually estimated and recorded the percent cover of yew and ferns (Evergreen Woodfern, *Dryopteris marginalis*) within a 3-m radius of each survey flag. In addition, we recorded the number of tree seedlings (<2.5 cm diameter breast height), yew stems, and percent fern cover within a 1-m quadrat at each survey flag.

We used paired *t*-tests (SAS Institute, Inc. 1990) to compare mean small mammal capture rates (number of individuals/100 adjusted trap nights) and mean vegetative values in yew and non-yew sites. Means are reported with ± 1 standard deviation; statistical significance was defined as $P < 0.05$.

We used three indices to compare species diversity of small mammals between yew and non-yew stands: Species Richness, Shannon-Weiner (*H'*), and Simpson's (λ) (Colinvaux 1986; Kirkland 1990). Species Richness (*S*) is a measure of the number of species actually documented by observation or capture. The Shannon-Weiner index (*H'*) is a measure of the probability of selecting the identity of an individual taken from the sample at random and uses the equation:

$$H' = -\Sigma\, p_i \ln p_i$$

Where p_i is the proportion of the total number of individuals in the *i*th species; *H'* increases with species diversity. Simpson's index (λ) is the probability that any two individuals selected at random will be the same species and uses the equation:

$$\lambda = \Sigma\, p_i^2$$

Simpson's index is actually an inverse measure of diversity in that species diversity increases as λ decreases.

Results

We captured 72 individuals representing five species in 2000 unadjusted trap nights (1000 each in yew and non-yew). Fifty-three individuals were captured in yew sites; 19 individuals were captured in non-yew sites. Mean capture rate/100 ATN was greater ($t_5 = 2.94$, $P = 0.04$) in yew sites (5.5 ± 2.2 individuals) than in non-yew sites (1.9 ± 1.0 individuals). The most common species captured in yew sites was Short-tailed Shrew (*Blarina brevicauda*, 45%), Deer Mouse (*Peromyscus maniculatus*, 26%) and Southern Red-backed Vole (*Clethrionomys gapperi*, 19%) (Figure 1). Short-tailed Shrew (42%) and Deer Mouse (47%) were the species most frequently captured in non-yew sites. Species diversity of small mammals was greater in stands with Canada Yew, with indices of $S = 5$, $H' = 1.31$, and $\lambda = 0.35$. Species diversity indices in stands without Canada Yew were $S = 4$, $H' = 1.01$, and $\lambda = 0.40$.

Average mean cover of yew in the 3-m radius plots at yew sites was 46 times greater than mean cover of yew in non-yew sites (Table 1). Mean number of yew stems/m^2 in yew sites was significantly greater than mean number of yew stems in non-yew sites. However, the number of Sugar Maple and total tree seedlings was significantly greater in non-yew sites. Percent fern cover in 1 m^2 and 3-m radius plots was similar in yew and non-yew sites.

Discussion

Although the mean number of hardwood seedlings was greater in non-yew stands, increased stem density and percent cover on study sites with Canada Yew provided greater understory structure in northern hardwood forests than did sites without yew. This difference in understory structure was likely responsible for observed differences in small mammal abundance and diversity. Increased structure caused by Canada Yew probably reduces the vulnerability of small mammals to predation through creation of physical barriers or visual obstruction. Several authors have suggested that small mammals use structure to avoid predation (e.g., Nordyke and Buskirk 1991; Kurta 1995).

Seeds of Canada Yew could also provide an important food source for small mammals, and conifer seeds are important food items for many rodent species (Ure and Maser 1982; Gunther et al. 1983). Arils and seeds of Canada Yew are reportedly eaten by Deer Mice (Wilson et al. 1996) which could explain the increased abundance of this species in yew sites. In addition,

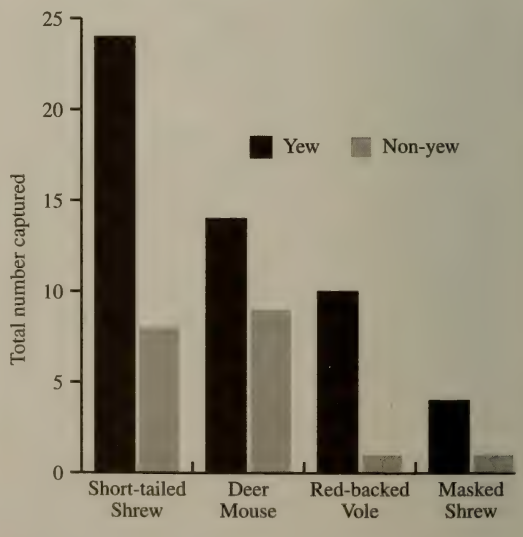


FIGURE 1. Number of individual small mammals captured in northern hardwood stands with and without understories containing Canada Yew ($n = 5$ sites/treatment), Upper Peninsula of Michigan, October-November 2000.

TABLE 1. Vegetative characteristics (mean ± SD) in northern hardwood stands with and without understories containing Canada Yew (n = 5 sites/treatment), Upper Peninsula of Michigan, October-November 2000.

	Yew		Non-yew			
Parameter	Mean	SD	Mean	SD	t	P
% Yew cover in 3-m radius plot	55.2	4.2	1.2	1.2	23.29	<0.001
Number of Yew stems in 1 m^2 quadrat	6.7	0.4	0.1	0.1	31.53	<0.001
Number of Sugar Maple seedlings	0.1	0.1	1.7	1.3	2.85	0.046
Number of American Beech seedlings	0.3	0.2	0.6	1.1	0.85	0.848
Number of other seedlings	0.2	0.2	0.4	0.2	0.92	0.408
Total number of seedlings[1]	0.5	0.2	2.8	1.4	3.31	0.030
% fern cover in 1 m^2 quadrat	5.6	2.7	4.8	0.9	0.51	0.637
% fern cover in 3-m radius plot	7.0	1.8	7.3	1.7	0.21	0.845

[1] rounding errors account for the 0.1 differences in total mean from sum of individual means.

increased structure and mesic conditions provided by Canada Yew may result in greater invertebrate numbers. Monthey and Soutiere (1985) found higher shrew numbers in logged forests with increased structure at ground level and associated this response to higher invertebrate numbers.

Presence of Canada Yew also affects microclimate by shading which results in increased moisture. Greater abundance of Red-backed Voles in yew sites probably reflects their preference for mesic sites and their comparatively high water requirements (Getz 1968; McManus 1974).

Loss of Canada Yew throughout much of its former range may have affected small mammal and other species abundance and distribution, particularly Red-backed Voles in hardwood forests. If patterns from this study are valid, the greatest effect from loss of yew would be localized reductions in shrew and Red-backed Vole populations. Continued increases in deer populations and human activities (e.g., clearing of land) could exacerbate this effect.

Acknowledgments

Funding for this study was provided by Pictured Rocks National Lakeshore. We thank Shelter Bay Forests, Incorporated, particularly Marty Wilk, for access to study sites.

Literature Cited

Allison, T. D. 1990. The influence of deer browsing on the reproductive biology of Canada yew (*Taxus canadensis* Marsh). I. Direct effect on pollen, ovule, and seed production. Oecologia 83: 523-529.

Beals, E. W., and **G. Cottam**. 1960. The forest vegetation of the Apostle Islands, Wisconsin. Ecology 41: 743-751.

Beauvais, G. P., and **S. W. Buskirk.** 1999. Modifying estimates of sampling effort to account for sprung traps. Wildlife Society Bulletin 27: 39-43.

Belant, J. L. 1992. Efficacy of three types of live traps for capturing weasels, *Mustela* spp. Canadian Field-Naturalist 106: 394-397.

Bent, A. C. 1963. Life histories of North American wood warblers. Part I. Dover Publications, New York, New York. 367 pages.

Colinvaux, P. A. 1986. Ecology. John Wiley and Sons, Inc., New York, New York. 725 pages.

Danz, N. P. 1998. Influence of Canada yew on population structure of sugar maple and beech. M.S. thesis, University of Minnesota, St. Paul, Minnesota. 76 pages.

Fordham, A. J. 1967. Seed dispersal by birds and animals in the Arnold Arboretum (Harvard University). Arnoldia 27: 73-84.

Frederick, D. J., L. Rakestraw, C. R. Eder, and **R. A. VanDyke.** 1977. Original forest vegetation of Pictured Rocks National Lakeshore and a comparison with present condition. Michigan Academician 9: 433-443.

Getz, L. L. 1968. Influence of water balance and microclimate on the local distribution of the redback vole and white-footed mouse. Ecology 49: 276-286.

Gunther, P. M., B. S. Horn, and **G. D. Babb.** 1983. Small mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. Northwest Science 57: 32-44.

Holmes, R. T. 1994. Black-throated blue warbler (*Dendroica caerulescens*). The Birds of North America, Number 87. *Edited by* A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia and The American Ornithologist's Union, Washington, D.C.

Kirkland, G. L., Jr. 1990. Patterns of initial small mammal community change after clearcutting of temperate North American forests. Oikos 59: 313-320.

Kurta, A. 1995. Mammals of the Great Lakes region. University of Michigan Press, Ann Arbor, Michigan. 376 pages.

Leopold, A., L. K. Sowls, and **D. L. Spencer.** 1947. A survey of over-populated deer ranges of the United States. Journal of Wildlife Management 11: 163-177.

Martell, D. L. 1974. Canada yew *Taxus canadensis* Marsh. U. S. Department of Agriculture Forest Service General Technical Report NE-1974: 158-160.

McManus, J. J. 1974. Bioenergetics and water requirements of the redback vole, *Clethrionomys gapperi*. Journal of Mammalogy 55: 30-44.

Monthey, R. W., and **E. C. Soutiere.** 1985. Responses of small mammals to forest harvesting in northern Maine. Canadian Field-Naturalist 99: 13-18.

Nordyke, K. A., and **S. W. Buskirk.** 1991. Southern redbacked vole, *Clethrionomys gapperi*, populations in relation to stand succession and old-growth character in the central Rocky Mountains. Canadian Field-Naturalist 105: 330-334.

SAS Institute, Inc. 1990. SAS/STAT User's Guide, Version 6. Fourth Edition. Cary, North Carolina. 1685 pages.

Snyder, J. D., and **R. A. Janke.** 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. American Midland Naturalist 95: 89-92.

Stachowicz, J. J., and **T. D. Allison.** 1995. Vegetation, browsing, and site factors as determinants of Canada yew distribution in central New Hampshire. Rhodora 97: 357-374.

Ure, D. C., and **C. Maser.** 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60: 3307-3315.

Wilson, P., M. Buonopane, and **T. D. Allison.** 1996. Reproductive biology of the monoecious clonal shrub *Taxus canadensis*. Bulletin of the Torrey Botanical Club 123: 7-15

Received 20 April 2001
Accepted 29 March 2004

Lack of Evidence for Impact of the European White Birch, *Betula pendula*, on the Hydrology of Wainfleet Bog, Ontario

JOSHUA DIAMOND[1], MARK BROWNING[2], ANDREW WILLIAMS[3], and JOHN MIDDLETON[4]

[1]Niagara Peninsula Conservation Authority, Welland, Ontario L3C 3W2 Canada
[2]Ontario Ministry of Natural Resources, Wildlife Research and Development Section, Peterborough, Ontario K9J 8M5 Canada
[3]School of Mathematics and Statistics, Carleton University, Ottawa, Ontario K1S 5B6 Canada
[4]Centre for the Environment, Brock University, St. Catharines, Ontario L2S 3A1 Canada

Diamond, Joshua, Mark Browning, Andrew Williams, and John Middleton. 2004. Lack of evidence for impact of the European White Birch, *Betula pendula*, on the hydrology of Wainfleet Bog, Ontario. Canadian Field-Naturalist 117(3): 393-398.

Over time peat harvesting and human encroachment have devastated the hydrology of Wainfleet Bog. Disturbances caused by human activities have rendered the bog ecosystem vulnerable to an influx of invasive species. The European White Birch (*Betula pendula*) has contributed to the degradation of the Wainfleet Bog. The disrupted hydrology has allowed for the development of dry conditions that have enabled *B. pendula* to take over habitats that were once dominated by native flora. To determine whether *B. pendula* was depressing the water table through evapotranspiration, we examined water table levels (March 1998 to July 1999) and vegetative data from 15 well stations. Analysis of results using a Repeated Measures Statistic Design failed to demonstrate a significant relationship between the presence of *B. pendula* and water table levels at Wainfleet Bog.

Key Words: *Betula pendula,* Wainfleet Bog, Ontario, birch, invasive species, hydrology, bog.

This study was designed to investigate the effects of the European White Birch (*Betula pendula*) on the hydrology of Wainfleet Bog. Wainfleet Bog is the largest wetland in the Niagara Region and its ecological value is significant. More than 80% of the wetlands in the Niagara Region have been converted to other land uses (Environment Canada 1986). Wainfleet Bog has not been spared human intervention. Over the last century more than one third of this bog has been lost to peat extraction and agricultural activities. However, this ecosystem still supports a variety of provincially rare species such as the Massasauga Rattlesnake (*Sistrurus catenatus catenatus*) (Niagara Peninsula Conservation Authority 1997). Most of the bog is now publicly owned and managed by the Niagara Peninsula Conservation Authority (NPCA), the Ontario Ministry of Natural Resources (MNR), and the Nature Conservancy of Canada (NCC). The shared goal of these agencies is to restore the Wainfleet Bog ecosystem to a healthy, less-disturbed state, providing recreational, educational and scientific opportunities for existing and future generations.

The disruption of the hydrology of Wainfleet Bog has been identified as the primary barrier to rehabilitating this ecosystem. The harvesting of peat severely impacted sections of the bog as the construction of drainage ditches and channels lowered the water table. According to Clymos and Hayward (1982), decreases to water table levels are catastrophic to *Sphagnum* spp. populations as they are unable to survive in these drier conditions and perish due to desiccation. In addition, the harvesting of peat changes the chemical composition (Wind-Mulder et al. 1996) of the bog, and removal of the viable seed bank through direct harvesting impairs the natural regeneration of bogs (Salonen 1987). All of these factors have created ideal conditions for *B. pendula* to invade this ecosystem.

Betula pendula is regarded as one of the five invasive plants that will have a major impact on the ecosystems of Canada (Environment Canada 1997). *B. pendula* is well described as a pioneer species in disturbed ecosystems in Spain (Reyes et al. 1997). The seeds of *B. pendula* are wind dispersed and have been reported to disperse between hundreds and thousands of metres (Reyes et al. 1997). Seeds usually prefer sunny places free from plant cover to germinate (Atkinson 1992). Areas which have been harvested for peat, or have been burned are ideal for establishment. Houle (1991) found the seeds of *B. pendula* form a persistent seed bank with a very high rate of renewal. Reyes et al. (1997) found *B. pendula* to grow quickly and reach a great height within a short time. Lavoie and Saint-Louis (1999) reported *Betula populifolia*, a pioneer species with similar ecological requirements to *B. pendula,* spreading throughout abandoned peatlands in eastern Quebec.

Betula pendula is naturally distributed throughout most of Asia and Europe, from Sicily to the 69°N in Norway (Atkinson 1992). However, it has been cultivated for many years in Canada by nurseries as an ornamental tree. Peat harvesting and decreases in water table level have allowed the invasion of *B. pendula* into the Wainfleet Bog ecosystem (Catling and Spicer 1988; Jonsson-Ninniss and Middleton 1991; MacDonald 1992). *B. pendula* is currently thriving in the present conditions found in this bog. Impenetrable forests of *B. pendula* dominate much of the landscape within Wainfleet Bog and cover an area of several hundred hectares.

The presence of *B. pendula* has been identified as a partial cause for the failure of the reestablishment of the Wainfleet bog hydrology. Lavoie and Saint-Louis (1999) suggested that massive invasions by birch trees into abandoned peatlands may have a detrimental effect on the water table. Schouwenaars (1988) also reported that evapotranspiration by trees and bushes impacts the water table level of disturbed bog relicts in the Netherlands. Furthermore, Kozlowski and Pallardy (1997) show that species in the genus *Betula* generally have a much higher transpiration rate than oak (*Quercus*), beech (*Fagus*) or the conifers such as spruce (*Picea*) and pine (*Pinus*). Consequently, there is great concern about the impacts that *B. pendula* and overall vegetation may be having on the bog hydrology. The purpose of this study was to examine the relationship of *B. pendula* and the water table level at Wainfleet Bog.

Study Area

Wainfleet Bog is the largest Class 1 provincially significant wetland in the Niagara Region, the highest rating according to the classification scheme set out by the Ontario Ministry of Natural Resources 1992. It is located near the towns of Port Colborne and Welland in southern Ontario. The bog is 1500 ha in size with peripheral areas of fen, marsh and swamp forest. It has an elevation between 175.5 m and 178.5 m on the Haldimand Clay Plain at latitude of 42°55'N and longitude of 79°17'W. The bog has an east-west length of approximately 5 km and a north-south expanse of approximately 3.5 km. Adjacent land uses around the perimeter include agriculture, quarrying, an industrial park and a major highway. Wainfleet Bog is relatively young and shallow with a maximum peat depth of 5 m, and approximate average peat depth of 3 m. Core and tests of the lowermost organic stratum suggest that the age of Wainfleet Bog is approximately 5000 years B.P. (Jonsson-Ninniss and Middleton 1991).

Over the last century, Wainfleet Bog has been extensively mined for peat moss using block cutting methods initially, and later vacuum harvesting. The central area of the bog is the most disturbed. Extraction of peat resulted in serious ecological impacts within the bog. The most disturbed areas were completely stripped of vegetation to expose the peat. Exposed peat was allowed to dry, and was then harvested using vacuum machinery. The bog's hydrology has also been severely altered through the construction of drainage ditches to facilitate the peat harvesting process. The only relatively undisturbed area within Wainfleet Bog has been designated an Area of Natural and Scientific Interest

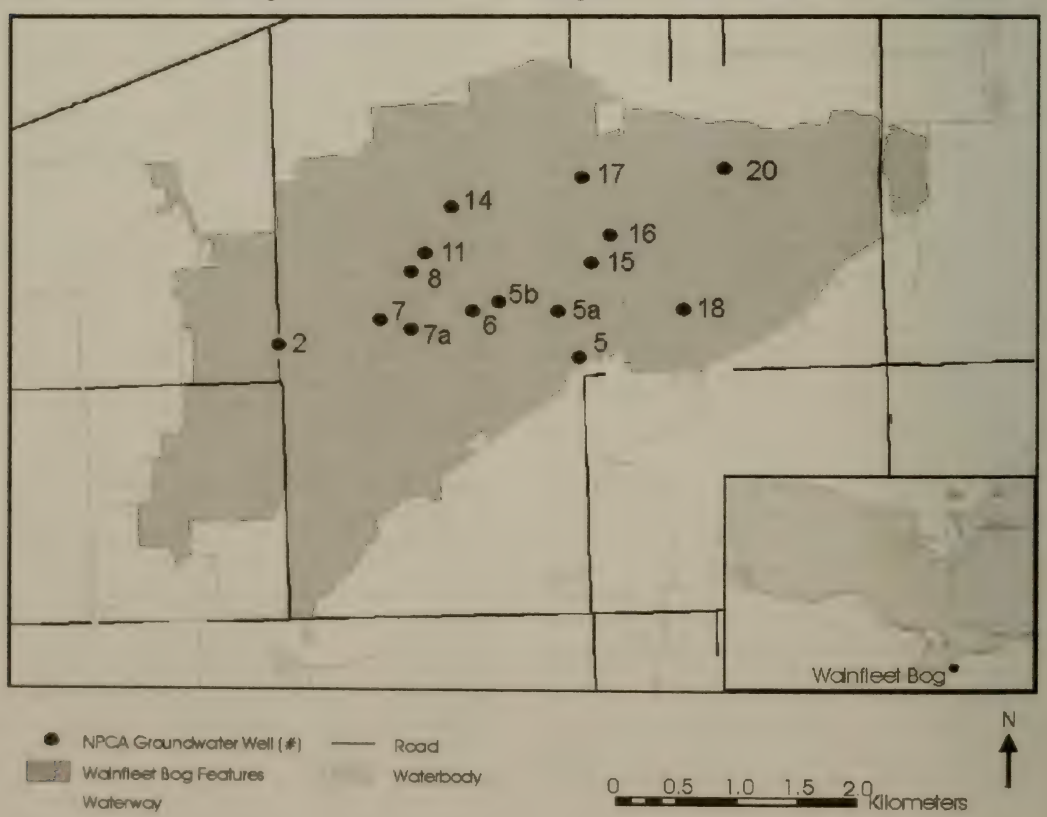


FIGURE 1. Location of groundwater well sites in Wainfleet Bog.

TABLE 1. Summary of the repeated measures Analysis of Variance for the presence of *Betula pendula* and other woody vegetation at Wainfleet Bog (P>0.05).

Source	Type III Sum of Error	df	Mean Square	F	P-value
B. pendula present	2.285	1	2.285	1.886	0.195
Non-*B. pendula* woody vegetation present	1.363	1	1.363	1.125	0.31
Error	14.542	12	1.212		

(ANSI). The ANSI is 200 ha in size and has not been subjected to direct peat harvesting or its related impacts. However, peat harvesting and drainage in the other sections of the bog have allowed for both a depression in the water table and the invasion of *B. pendula* in the ANSI.

Trembling Aspen (*Populus tremuloides*), birch (*Betula* spp.) and Black Cherry (*Prunus serotina*) form a forest belt between the interior of the bog and the surrounding farm land (Jonnson-Ninniss and Middleton 1991). Disturbed areas of the bog may be free of living vegetation, dominated by the tall ericacious shrubs *Aronia melanocarpa* and *Vaccinium corymbosum*, or have a closed canopy of primarily *B. pendula*. In the most recent, vacuum-mined sites often only three species are present: hair-cap moss (*Polytrichum strictum*), bunch cotton-grass (*Eriophorum vaginatum*) and *B. pendula*. The least disturbed areas are open with a few scattered trees; ground cover is predominately *Sphagnum* mosses and ericacious shrubs.

Methods

To monitor water level fluctuations at Wainfleet Bog, the Niagara Peninsula Conservation Authority (NPCA) set up 25 well stations. These wells were made of 5 cm diameter PVC pipe and were distributed throughout the bog. Water level data have been collected by the NPCA on a near-monthly basis from March 1998 to the present. For this study, well station data were used from 31 March 1998, 4 June 1998, 17 June 1998, 2 July 1998, 16 July 1998, 30 July 1998, 27 August 1998, 24 March 1999, 15 April 1999, 19 May 1999, 2 June 1999, and 16 June 1999. On several occasions the water level at various well stations was too low to be detected and resulted in no water level reading for that particular observation. Subsequently observations of this nature were removed from the data set.

Vegetative data were collected at 15 existing well stations distributed throughout the bog (Figure 1). At each well station a compass bearing of northeast was taken. From each well station, following the northeast bearing, 11.28 m was measured out to point A. Point A became the centre of a circular plot of 11.28 m radius (1/25 ha). Around point A starting at due north (0 degrees) and moving east, all trees were numbered consecutively with tree paint. Any living trees with a diameter at breast height (dbh) of 9.5 cm dbh and within the 1/25 ha circular plot were counted. Trees forked at or below breast height counted as two trees. The dbh of all trees greater than 9.5 cm was recorded. All trees surveyed in this circle plot were identified to species.

In addition to the circle plot, a 10 m by 10 m square plot was set up for each well station. Point A was used as the centre of this plot. Orientation of this plot was set to due north. This 10 m by 10 m plot was divided to form ten 1 m by 10 m plots. One of these 1 m by 10 m plots was selected randomly, and all saplings or shrub stems less than 9.5 cm dbh and greater than 1 m in height were counted and identified. No dbh data were taken for these smaller trees.

The data in this study were analyzed with a Repeated Measures Design (Johnson and Wichern 1992). The assumptions for this statistical procedure were tested utilizing the Kolmogorov-Smirnov Test of Normality, and Levene's Test of Equality of Error Variance. Each of these assumptions was met. Well stations were assumed to be independent when the distance between each well station was greater than 10 metres, based on hydrological studies of the bog (NCPA: Wainfleet Bog Hydrological Assessment Meeting, unpublished data). All stations used in this study were separated by a minimum of 10 m.

Invasion by woody vegetation, and specifically *Betula* spp. in abandoned peatlands, has been reported as having the potential to have detrimental effects on the water table (Lavoie and Saint-Louis 1999). The statistical design developed for this analysis tested the null hypothesis that vegetation (particularly *B. pendula*) and water table level are independent. A summary of the statistical design is found below. The biological predications of this study were that plots with a high population of *B. pendula* would have a lower water table level due to the effects of evapotranspiration, while plots with a low population of *B. pendula* would have higher water table levels.

Statistical Design

Water Level = Intercept (Mean Water Level) + Effect Due to Presence of *B. pendula** + Effect Due to Presence of Other Woody Vegetation•

* Represents an effect due only to the presence of *B. pendula.*

• Represents an effect due to the presence of all other woody vegetation not including *B. pendula.*

Results and Discussion

The results of the Repeated Measures Design failed to demonstrate a significant relationship between *B. pendula* (ANOVA, P>0.05) or non-*B. pendula* vegetation (ANOVA, P>0.05) and water table level (Table 1). A summary of the data can be found in Table 2. According to Schouwenaars (1993), the groundwater in bog ecosystems reaches the surface during most of the winter period, and this water should not be deeper than 30-40 cm in the summer. In Figure 2, several well stations (5, 8, 18) had no *B. pendula* and minimal non-*B. pendula* vegetation, yet water table levels remain lower than the range of levels suggested by Schouwenaars in a healthy bog ecosystem. In comparison, station 2 has a water table level within the range suggested by Schouwenaars, yet there are a substantial number of trees present at this site, although only two are *B. pendula*. These findings would suggest that *B. pendula* and non-birch woody vegetation are not the primary factors affecting the water table level of Wainfleet Bog. However, the cause of the variation in birch tree density in the bog remains obscure and probably involves factors other than the obvious ones of water table level and length of regeneration.

Cross (1987) observed an unusual stand of birch trees growing successfully on a moderately disturbed bog in Ireland (All Saints Bog). It is 230 ha in size, and has a plant community typical of a raised bog ecosystem. The water table of this bog is at the surface, and the peat has a pH of 4.0. Within this bog, a well-developed 20 ha birch community made up of *B. pendula* and *B. pubescens* exists. Cross observed no significant effects of the birches on the water table in this community. However, Schouwnaars (1988) does indicate evapotranspiration should not be ruled out of any hydrological modelling when considering bog restoration.

The most damaging attribute of *B. pendula* is the occupation of habitats that regenerating bog vegetation would normally occupy. The scale of the birch tree infestation in the regenerating areas of the bog is large, with trees extending thickly over several hundred hectares (Figure 3). This invasion of *B. pendula* has led to the destruction of open bog vegetation as non-acidic deciduous leaf litter often buries the bog plants (MacDonald 1992). The decomposition of such leaf litter is contributing excessive nutrients to the bog which, under undisturbed conditions, would be nutrient deficient. In addition, the birch forest canopy is intercepting light that would normally reach the bog vegetation and this should also be considered a substantial impact (MacDonald 1992). Further studies of *B. pendula* that quantify its exact mechanism of impact are necessary if restoration of the *Sphagnum* layer is to be attempted.

Recent findings by the NPCA (unpublished data) suggest that the hydrology is most affected by the series of interior and exterior drainage ditches which

TABLE 2. Summary of vegetative and well station data for Wainfleet Bog.

Well Station Number	Number of Observations	Surface Elevation (m)	Mean Water Table Level (m)	Minimum (m)	Maximum (m)	Standard Deviation	Number of all *Betula pendula* trees & saplings per Well Station	Total DBH of *Betula pendula* (cm)	Number of all of non-*Betula pendula* trees & saplings	Total DBH Non-*Betula pendula* (cm)
2	8	175.42	175.41	175.20	175.50	0.1207	0	0	18	732.1
5	8	176.11	175.33	175.00	176.45	0.4609	0	0	8	291.1
5a	8	175.68	175.17	174.39	175.73	0.3481	4	64.96	97	11.3
5b	8	176.22	175.71	175.37	175.96	0.2074	10	0	71	0
6	8	176.49	175.84	175.70	176.16	0.1889	5	28	77	128.5
7	8	176.06	175.72	175.70	176.09	0.1597	7	0	0	0
7a	8	175.88	175.33	174.89	175.89	0.2688	99	0	7	0
8	8	176.06	175.24	174.94	175.57	0.2395	19	148.4	6	0
11	8	175.98	175.49	175.22	175.70	0.1521	0	0	0	0
14	8	176.42	175.96	175.02	176.00	0.1027	0	0	0	0
15	8	175.47	174.76	174.30	175.28	0.3875	0	0	38	61.6
16	8	175.82	175.27	174.97	175.55	0.2048	14	0	39	18
17	8	176.61	175.89	175.76	176.12	0.1505	0	0	9	109.1
18	8	176.24	175.22	174.67	175.47	0.2769	0	0	2	25.2
20	8	176.35	175.67	175.51	175.87	0.1131	2	20.1	156	0

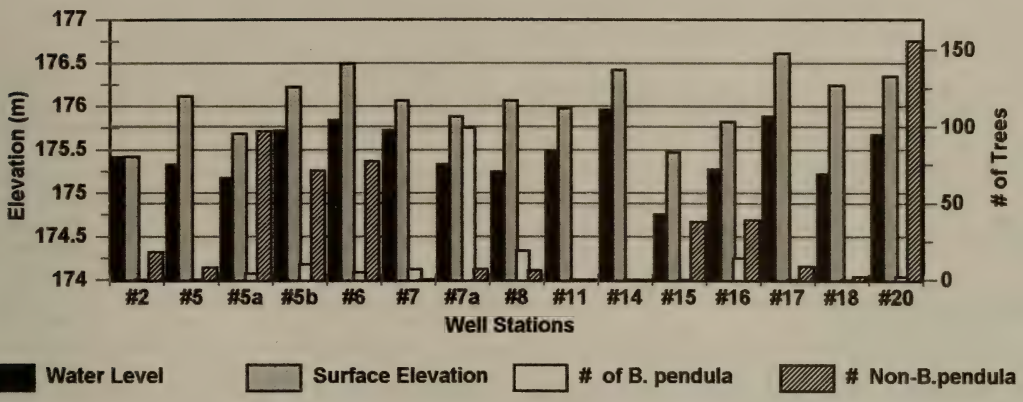


FIGURE 2. Surface elevation, mean water (31 March 1998 –16 June 1999), and the number of *B. pendula* and non-*B. pendula* found at each well station.

FIGURE 3. *Betula pendula* in the regenerating areas of Wainfleet Bog.

still exist in Wainfleet Bog. It is possible that restoration of the bog hydrology can be obtained by filling and dismantling these drainage ditches. However, this strategy is being initiated gradually as organisms such as the Massasauga Rattlesnake may have become dependent upon the altered drier conditions of the bog. It is also not entirely clear whether higher water table levels would provide a control solution as *B. pendula*

has been found to inhabit undisturbed bog conditions (Cross 1987). Other strategies for controlling *B. pendula* in the bog, as well as other hydrology studies, are currently under way (NPCA, unpublished data).

We conclude that the results of this study failed to demonstrate a significant relationship between the presence of *B. pendula* or other woody vegetation with water table level in Wainfleet Bog. The population of *B. pendula* at Wainfleet Bog is alarming for many ecological reasons, but its direct impact on hydrology remains to be demonstrated.

Acknowledgments

We thank Kim Frohlich and Geoff Verkade of the Niagara Peninsula Conservation Authority for providing us with water well data and various other resources. We are also very grateful for the assistance of Karen Krug of Brock University for her comments on the earlier parts of this study.

Literature Cited

Atkinson, M. D. 1992. *Betula pendula* Roth (*B. verruscosa* Ehrh.) and *B. pubescens* Ehrh. Journal of Ecology 80: 837-870.

Catling, P. M., and **K. W. Spicer.** 1988. The separation of *Betula populifolia* and *Betula pendula* and their status in Ontario. Canadian Journal of Forest Research 18: 1017-1026.

Clymos, R. S., and **P. M. Hayward.** 1982. The Ecology of *Sphagnum*. Pages 229-289 *in* Bryophyte Ecology. Chapman and Hall, New York.

Cross, J. A. 1987. Unusual stands of birch on bogs. Irish Naturalist Journal 22: 305-310.

Environment Canada. 1986. Canada's wetlands: National Wetland Group. Canada Committee on Ecological Land Classification, Environment Canada, Ottawa.

Environment Canada. 1997. Conserving vitality and diversity: proceedings of World Conservation Congress, workshop on alien species. Environment Canada, Ottawa.

Houle, G. 1991. Regeneration traits of tree species in deciduous forest of northern North America. Holarctic Ecology 14: 142-151.

Johnson, R. A., and **D. W. Wichern.** 1992. Applied multivariate statistical analysis. Prentice Hall, New Jersey.

Jonsson-Ninniss, S., and **J. Middleton.** 1991. Effect of peat extraction on the vegetation in Wainfleet Bog, Ontario. Canadian Field-Naturalist 105: 505-511.

Kozlowski, T. T., and **S. G. Pallardy.** 1997. Physiology of woody plants. Second edition. Academic Press, San Diego.

Lavoie, C., and **A. Saint-Louis.** 1999. The spread of gray birch (*Betula populifolia*) in eastern Quebec: landscape and historical considerations. Canadian Journal of Botany 77: 859-868.

MacDonald, I. D. 1992. A biological inventory and evaluation of the Wainfleet Bog Area of Natural and Scientific Interest. Ministry of Natural Resources, Ontario.

Niagara Peninsula Conservation Authority. 1997. Wainfleet Bog management plan, Wainfleet Ontario. Niagara Peninsula Conservation Authority, Welland, Ontario.

Ontario Ministry of Natural Resources and Ministry of Rural Affairs. 1992. Manual of implementation guidelines for the Wetlands Policy Statement. Toronto, Ontario.

Reyes, O., M. Casal, and **L. Trabaud.** 1997. The influence of population, fire and time of dissemination on the germination of *Betula pendula* seeds. Plant Ecology 133: 201-208.

Salonen, V. 1987. Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. Holarctic Ecology 10: 171-174.

Schouwenaars, J. M. 1988. The impact of water management upon groundwater fluctuations in a disturbed bog relict. Agricultural Water Management 14: 439-449.

Schouwenaars, J. M. 1993. Hydrological differences between bogs and bog-relicts and consequences for bog restoration. Hydrobiologia 265: 217-224.

Wind-Mulder, H. L., L. Rochefort, and **D. H. Vitt.** 1996. Water and peat chemistry comparisons of natural and post-harvested peatlands across Canada and their relevance to peatland restoration. Ecological Engineering 7: 161-181.

Received 6 July 2001
Accepted 17 March 2004

Historical Changes and Current Distribution of Caribou, *Rangifer tarandus*, in Quebec

Rehaume Courtois[1,2,3], Jean-Pierre Ouellet[2], André Gingras[4], Claude Dussault[5], Laurier Breton[1] and Jean Maltais[6]

[1]Société de la faune et des parcs du Québec, Direction de la recherche sur la faune, 675, René-Lévesque, Est, 11e étage, boîte 92, Québec, Québec G1R 5V7 Canada; e-mail: rehaume.courtois@fapaq.gouv.qc.ca
[2]Université du Québec à Rimouski, Département de biologie et des sciences de la santé, Centre d'études nordiques, 300, Allée des Ursulines, Rimouski, Québec G5L 3A1 Canada
[3]Université Laval, Département de foresterie et de géomatique, Cité Universitaire, Ste-Foy, Québec G1K 7P4 Canada
[4]Société de la faune et des parcs du Québec, Direction de l'aménagement de la faune, 818, boulevard Laure, Sept-Îles, Québec G4R 1Y8 Canada
[5]Société de la faune et des parcs du Québec, Direction de l'aménagement de la faune, 3950 boulevard Harvey, 4e étage, Jonquière, Québec G7X 8L6 Canada
[6]Conseil de l'industrie forestière du Québec, 1175, avenue Lavigerie, Bureau 200, Sainte-Foy, Québec G1V 4P1 Canada

Réhaume Courtois, Jean-Pierre Ouellet, André Gingras, Claude Dussault, Laurier Breton, and Jean Maltais. 2003. Historical changes and current distribution of Caribou, *Rangifer tarandus*, in Quebec. Canadian Field-Naturalist 117(3): 399–414.

We examined published historical information, reports on aerial surveys conducted since 1953, and harvest data collected since 1971 to describe changes in the distribution and abundance of Caribou (*Rangifer tarandus*) in Québec. The southern limit of the Caribou distribution diminished considerably in the late 19th century, and the decline in numbers probably continued until the 1960s and 1970s east of the 62nd meridian. South of the 49th parallel, only four small populations still persist. Despite the fact that all Caribou of the province were assigned to the same sub-species (*R. t. caribou*), three ecotypes with specific habitats and behaviour are found. The Barren-Ground ecotype, the only migratory form, is found north of the 52nd parallel. This ecotype currently occupies ≈ 255 000 km^2 in fall and winter, mainly in the ecological subzones of the forest tundra and the taiga. The Barren-Ground Caribou was characterized by a very low abundance from the end of the 19th century until the mid-1950s, but increased markedly thereafter reaching over a million individuals at the beginning of the 1990s. Populations of the Mountain ecotype have been identified in the southeastern and, possibly, in the northeastern parts of the province. The latter Mountain population is virtually unknown. The southeastern population is sedentary and uses mainly the boreal forest. This population has decreased over the last century and currently numbers only ≈ 140 individuals. Finally, the Forest-Dwelling ecotype is found discontinuously, mainly between the 49th and 55th parallels. Its current distribution covers ≈ 235 000 km^2, mainly east of the 72nd meridian. This sedentary ecotype is found almost exclusively in the boreal forest, principally in areas with long forest fire cycles. Its abundance has also decreased over the years. Large Forest-Dwelling populations still persisted during the 1950s and 1960s, but they apparently disappeared. The current abundance is not known precisely, but based on density estimates and considering the current distribution, it probably does not exceed 3000 individuals. Current data are insufficient to identify precisely the causes of the population decline, although hunting seems to be an important proximal cause.

Key Words: Caribou, *Rangifer tarandus*, Moose, *Alces alces*, distribution, ecotype, history, hunting, Québec.

Nous avons utilisé les données historiques publiées, les rapports d'inventaires aériens réalisés depuis 1953 et les statistiques de récolte sportive colligées depuis 1971 pour décrire les changements dans la répartition et l'abondance du Caribou (*Rangifer tarandus*) au Québec. La limite méridionale de l'aire de répartition a beaucoup diminué à la fin du 19e siècle et la régression s'est probablement poursuivie durant les années 1960 et 1970 à l'est du 62e méridien. Au sud du 49e parallèle, on ne retrouve plus que quatre petites populations. Bien que tous les caribous du Québec soient considérés appartenir à la même sous-espèce (*R. t. caribou*), on distingue trois écotypes fréquentant des milieux différents et arborant des comportements spécifiques. Au nord du 52e parallèle, on retrouve l'écotype Toundrique, lequel est migrateur. Ces Caribous se répartissent sur ≈ 255 000 km^2 durant l'automne et l'hiver, principalement dans les sous-zones écologiques de la toundra forestière et de la taïga. Cet écotype était peu abondant entre la fin du 19e siècle et le milieu des années 1950, mais il s'est accru considérablement pour atteindre plus d'un million d'individus au début des années 1990. Une population de l'écotype Montagnard est présente au sud-est de la province et une autre existe possiblement au nord-est. Cette dernière n'est pas bien connue. Celle du sud-est utilise principalement la forêt boréale. Cette population sédentaire a diminué considérablement depuis une centaine d'années et elle ne compte plus qu'environ 140 individus. Finalement, l'écotype Forestier est présent de façon discontinue, principalement entre les 49e et 55e parallèles. Ces Caribous sont également sédentaires. On les retrouve presque exclusivement en forêt boréale, principalement là où le cycle des feux de forêt est long. Leur répartition actuelle couvre ≈ 234 000 km^2, principalement à l'est du 72e méridien. D'importantes populations forestières existaient encore durant les années 1950 et 1960, mais elles semblent avoir disparu. L'abondance actuelle n'est pas connue mais elle pourrait difficilement dépasser 3000 individus si l'on se base sur les estimations de la densité et de l'aire de répartition. Les données disponibles sont insuffisantes pour identifier les causes exactes des diminutions d'effectifs bien que la chasse semble une cause proximale importante.

Mots clés : Caribou, *Rangifer tarandus*, Orignal, *Alces alces*, chasse, écotype, historique, Québec, répartition.

In North America, the oldest fossils of Caribou (*Rangifer tarandus*) are 50 000 years old (Banfield 1961; Brassard 1979). The species appears to have been abundant in the taiga, from the edge of the glaciers to New Mexico. Subsequent climatic changes seem to have considerably modified its distribution. At the arrival of the first Europeans, Caribou were found in areas currently occupied by all the Canadian provinces as well as the American states bordering on Canada. In the eastern part of the continent, Caribou were found in the present-day states of New York, Vermont, New Hampshire and Maine (Moisan 1956). However, today the Gaspésie Caribou population in eastern Quebec is the only remaining population south of the St. Lawrence River.

Despite the fact that all Caribou of the province were assigned to the same sub-species (*R. t. caribou*), three ecotypes (Barren-Ground, Mountain, Forest-Dwelling) can be identified based on habitat use, behaviour and genetics (Courtois et al. 2003). Many studies have examined the abundance, population dynamics and habitat of the Barren-Ground Caribou in northern Quebec and of the Gaspésie Mountain Caribou. The spectacular increase in numbers of the first ecotype and the precarious status of the second have made them favourite subjects for limitation and regulation mechanism studies (Messier et al. 1988; Crête and Desrosiers 1995; Couturier et al. 1996; Crête et al. 1996). Some studies have also been carried out on northern populations affected by hydroelectric developments (Brown et al. 1986; Paré 1987) and on the isolated populations in southern Quebec (Vandal 1985; Jolicoeur 1993*; Paré and Brassard 1994*; Crête and Desrosiers 1995; Ouellet et al. 1996). However, the Forest-Dwelling Caribou in the central part of the province remains largely unknown. Studies carried out on these populations are limited to surveys conducted in the 1960s and 1970s and, as no synthesis of available data has been done, their current distribution and status remain speculative.

This study had three main objectives: (1) to provide a comprehensive analysis of available data on Caribou in order to describe historical changes in Quebec; (2) to determine the current distribution of Caribou with the aim of identifying areas where this species should be considered a priority in forest management, and (3) to explore potential causes of temporal changes in Caribou abundance. As the magnitude of the harvest provides a relative index of abundance (Crête and Dussault 1987), we used harvest data to verify whether Caribou and Moose (*Alces alces*) harvests were inversely correlated. Because Wolf (*Canis lupus*) and Moose abundance are positively correlated (Messier 1994, 1995; Larivière et al. 2000), a decrease in Caribou harvest while Moose were increasing would suggest that Caribou abundance could be limited by Wolf predation (Bergerud 1974, 1988; Martin 1980; Bergerud and Mercer 1989; Jolicoeur 1993*; Seip 1992). Otherwise, Caribou could be limited to a greater extent by changes in harvest rate.

Methods

The historical distribution range was determined using published information (newspaper articles, activity reports, legislation and interviews; Moisan 1956; Martin 1980; Guay 1983; Bellehumeur et al. 1985*; Gingras et al. 1989; Jolicoeur 1993*). The distribution and abundance of Caribou from the 1950s to the 1970s were derived from 42 aerial survey reports (> 70 surveys). Various techniques were used. Until the early 1980s, surveys mainly consisted of systematic coverage of large blocks (9000 to 92 700 km^2) carried out between late February and mid-April, by airplane (Dornier 28-B, DC-3, Cessna 185), using north-south or east-west transects spaced 16.1 km apart at an altitude of 250-350 m (Brassard 1967*; Le Hénaff 1976a,b*). Animals were counted from each side of the aircraft at a distance of 500 m. The crews included a pilot, a navigator-observer and two other observers seated in the rear of the aircraft. The crews abandoned the flight lines to count all the Caribou when large groups (>75 individuals) or extensive track networks were observed (Le Hénaff 1976a*). The study sites were then post-stratified according to the numbers observed (population ≥ 75 individuals; scattered Caribou). The average density calculated for the transects in each stratum were extrapolated to obtain the total population per stratum and for the entire study area, without calculating the confidence interval or correcting for the visibility bias. The counts were likely underestimates, but these surveys provide a reliable picture of the distribution of Caribou on a regional scale. Beginning in the 1970s, surveys were carried out using sample plots, usually of 60 km^2, in order to calculate the variance of the estimates (Joly and Brassard 1980*; Brassard 1982*; Barnard 1983*; Gingras and Malouin 1993*; Bourbonnais et al. 1997*).

Caribou observations have been obtained through various sources since 1954 by the Société de la faune et des parcs du Québec (FAPAQ) and stored in a geographic information system (Anonymous 1996). The database includes 3825 records (< 1980: 436 records; 1980-1989: 1344; 1990-1999: 2045) from aerial surveys of Caribou conducted within limited areas (1333), chance observations made by individuals or aircraft pilots or by FAPAQ personnel (967), during aerial surveys of Moose (98), and finally, observations made during telemetry work in various regions (1427). Sport and subsistence hunting (234 191), as well as other known causes of mortality (e.g., poaching, road accidents, some cases of predation: 1302) documented since 1971 (Sebbane and Courtois 2001*) were also included. To give equal weight to the various sources of information, data were utilized in the form of a presence/absence index calculated for every 10 km^2 of the

*Internal reports are listed in the Document Cited section

province. Zones of continuous distribution were identified by means of the fixed kernel method using the 90% distribution probability, a grid cell of 0.1 and a smoothing factor of 0.4 (Hooge and Eichenlaub 1997). The same technique with 70% distribution probability was used to determine the extent of the zones of intensive use. Kernels were superimposed onto ecological (Anonymous 2000*) and forest fire cycle maps (Gauthier et al. 2001) to identify ecological zones, sub-zones and forest fire cycle of areas frequented by Caribou.

Finally, the sport harvest was used to describe changes that have occurred since 1971, in terms of abundance (Caribou harvested) and population structure (males and calves per 100 females, % of calves), in the zones of intensive use. The fall (1 August – 30 November) and winter (1 December – 30 April) harvests were considered separately when two hunting seasons existed. Characteristics of the harvest are likely to differ during the two seasons since the winter hunt mainly targets Barren-Ground Caribou. The Spearman coefficient was used to test the relationships between Caribou and Moose harvests as well as between Caribou harvest and productivity (% of calves, calves per 100 females) and harvest rate (males per 100 females) indices derived from hunting statistics. Correlation analyses were conducted for the 1971-1999 period, for each population separately.

Results

Historical Trends

In Québec, the first explorers noted the presence of Caribou on both shores of the St. Lawrence River, from the present-day location of Québec City (46° 48' N, 71° 15' W) to Gaspé (48° 49' N, 64° 30' W), and over the entire Laurentian plateau, in the centre of the Québec-Labrador peninsula (Martin 1980; Jolicoeur 1993*) (Figure 1). Initially, the Caribou was not heavily exploited, but hunting increased during the 19th century with the growth of the human population and as the colonists moved farther into the backcountry. The Caribou had disappeared from the St. Lawrence valley by 1850 (Martin 1980; Guay 1983). However, between 1865 and 1875, it could still be found on the north shore of the St. Lawrence River (Laurentides National Park, 47° 44' N, 71° 26' W; Montréal, 45° 33' N, 73° 39' W; Outaouais, 45° 42' N, 76° 00' W; Saint-Maurice, 46° 37' N, 72° 43' W) and from the Matapedia valley (48° 22' N, 67° 29' W) to the eastern part of the Gaspé Peninsula (Moisan 1956; Guay 1983; Gingras et al. 1989). By the early 20th century, the Caribou was already rare in inhabited areas, even in the Québec City region and farther east, as far as the Matapedia valley (Guay 1983). Hunting remained significant in the eastern part of Laurentides National Park (the part occupied today by Parc des Grands-Jardins: 47° 48' N, 70° 49' W) up until 1914, but the Caribou also disappeared from that area during the 1920s (Jolicoeur 1993*).

The situation evolved in a similar manner in the Saint-Maurice valley. For example, Caribou were observed and hunted regularly by the Triton Club up until the early 20th century, but were considered rare by 1915 (Gingras et al. 1989). It was only observed exceptionally after 1920, although one Caribou was observed in 1941, after many years with no sightings. The same situation was noted in southwestern Quebec. Caribou were still found there in the late 1800s, but seem to have been heavily exploited (Guay 1983). Further north, in Témiscamingue (46° 48' N, 79° 00' W) and Abitibi (48° 15' N, 79° 02' W), Caribou probably decreased in abundance at the beginning of colonization, during the 1920s-1930s. In eastern Ontario, Cumming and Beange (1993) place the southern limit of the Caribou at about the 48th parallel in 1900, at the 49th in 1950, and at the 50th in 1990. The trends were probably similar in western Quebec.

In northern Quebec, the narrative history of the Native peoples suggests the presence of three populations, one near Hudson Bay in the region of lakes Guillaume-Délisle (56° 15' N, 76° 30' W) and à l'Eau Claire, a second population to the east, which spent the summer on the high plateaus of Labrador and migrated to the George River (55° 16' N, 65° 53' W) in winter, and a third population which moved between summer and winter, from southern Ungava Bay (58° 37' N, 67° 48' W) to the Caniapiscau River (54° 48' N, 69° 50' W), in east-central Quebec (Brassard 1979). These populations are thought to have decreased between the mid-19th century and the mid-1950s, but then to have increased, similarly to other northern populations (Bergerud 1988; Couturier et al. 1996; Morneau and Payette 1998). In contrast, the southern Forest-Dwelling populations apparently did not recover.

Recent Trend According to Aerial Surveys

The first aerial surveys carried out in Quebec were regional in scope. In 1953 and 1954, Moisan (1957) surveyed the Gaspésie Caribou population, which then comprised between 700 and 1500 Caribou. Two surveys were carried out in northern Quebec in 1954 and 1956, and the population of the Ungava Peninsula was then estimated at 6120 Caribou (Banfield and Tener 1958). In 1963, Desmeules and Brassard (1963*) estimated that 60 000 Caribou were living in central and eastern Quebec.

The first wild ungulate aerial survey program was carried out between 1963 and 1968 (Brassard 1968*). It confirmed a reduction in the distribution range of Caribou in Quebec. South of the 49th parallel, only two isolated populations were found, in Gaspésie and Val-d'Or. Farther north, numerous isolated groups (called scattered Caribou by the author) and four areas of high concentration were found: one on the North Shore at the Labrador border, two in central Quebec in the Bienville and Caniapiscau Lake regions, and finally, one in the northeastern part of the province at the Labrador border. The total population of the

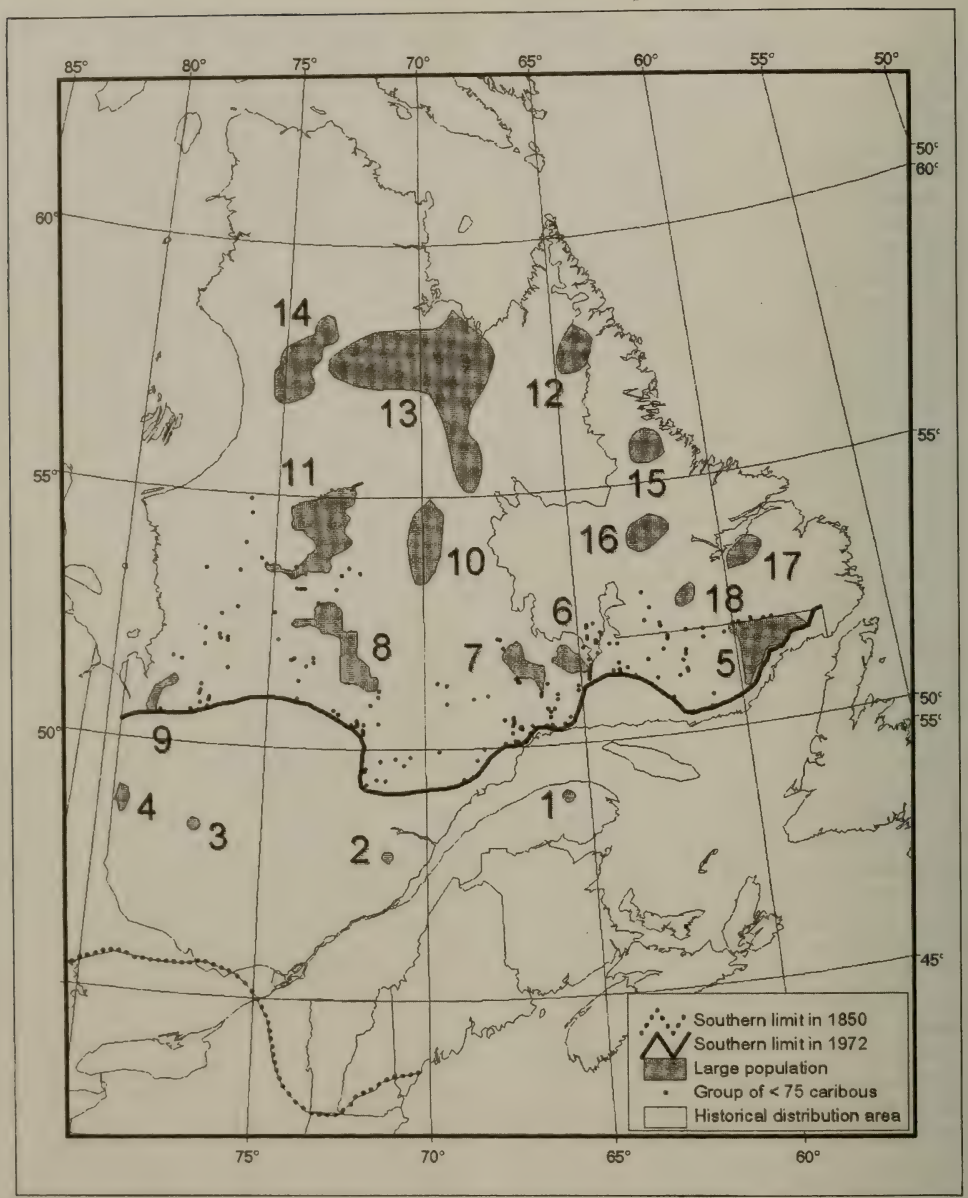


FIGURE 1. Distribution of Caribou in Quebec and adjacent jurisdictions before 1850 and in 1972-1973. Numbers refer to main populations located in 1972 and 1973: (1) Gaspésie; (2) Charlevoix; (3) Val-d'Or; (4) La Sarre; (5) Saint-Augustin; (6) Magpie River (Lac Joseph); (7) Petit Lac Manicouagan; (8) Mistassini Lake; (9) Rupert; (10) Caniapiscau Lake; (11) Bienville Lake; (12) Torngat Mountains; (13) George River (spring); (14) Leaf River; (15) George River (winter); (16) Red Wine Mountains; (17) Mealy Mountains; (18) Dominion Lake (Bergerud 1967; Brassard 1968*, 1972*, 1979, 1982*; Pichette and Beauchemin 1973*; Barnard 1983*; Paquet 1997*).

province was then estimated at between 68 000 and 90 000 Caribou, spread over an area of 1 007 432 km^2 (7-9 Caribou/100 km^2).

The first exhaustive inventories were carried out in 1972 and 1973, when Quebec and Labrador were entirely covered from the 49th parallel up to Hudson Strait (Brassard 1972*; Pichette and Beauchemin 1973*). The northern populations appeared to be concentrated between the south of Ungava Bay and the east of Hudson Bay (Figure 1). About 20 Forest-Dwelling populations were identified, of which six comprised a few hundred to a few thousand Caribou. At that time the

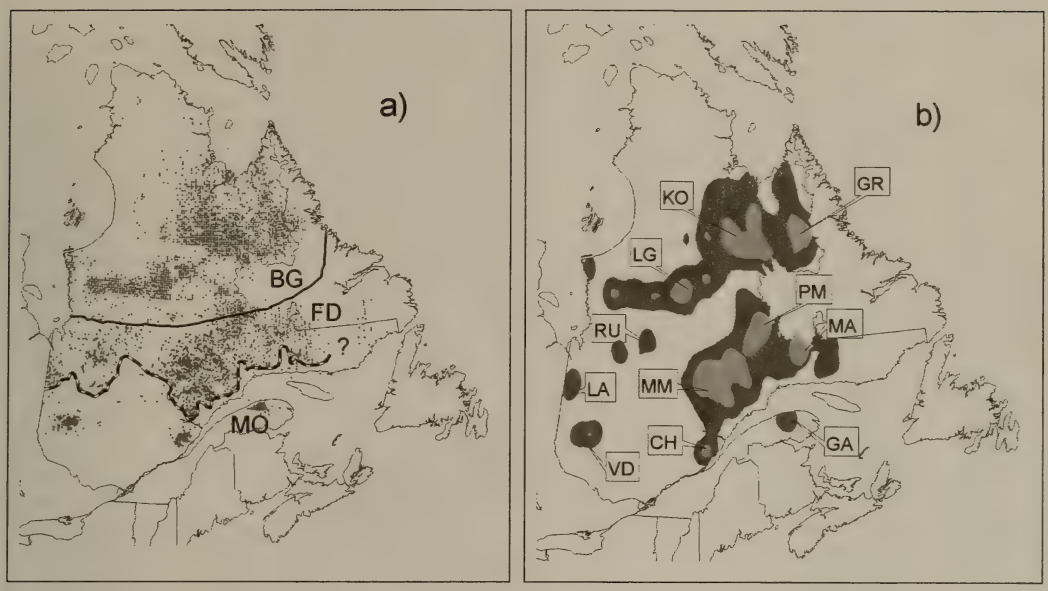


FIGURE 2. Main areas frequented by Caribou in Quebec. (a) presence per 10 km^2; and southern limit of Barren-Ground (BG: solid line), Forest-Dwelling (FD: broken line) and Mountain (MO) ecotypes distribution; southern limit of Forest-Dwelling ecotype unknown in eastern Quebec (?); (b) zones of continuous distribution (90% kernels) and zones of intensive use (70% kernels) of Barren-Ground (KO: Koksoak; LG: LG-4; GR: George River), Mountain (GA: Gaspésie) and Forest-Dwelling (CH: Charlevoix; VD: Val-d'Or; LA: La Sarre; RU: Rupert; MM: Manouane-Manicouagan; PM: Petit Lac Manicouagan; MA: Magpie) ecotypes.

Quebec population had been estimated at ≈ 120 000 Caribou north (16.5/100 km^2) and 12 000 south (3.7/100 km^2) of the 52nd parallel (Brassard 1979).

Subsequent surveys, usually carried out in the high concentration areas identified in 1972 and 1973, showed an expansion in the northern populations and a reduction in the southern ones. The northern Barren-Ground Caribou numbers rose from 3500 in the mid-1950s to about 1 000 000 individuals in 1993 (Couturier et al. 1996). The southern populations, more dispersed and sometimes rather indistinct, were monitored less intensively. The Gaspésie (140-200 Caribou) and Charlevoix (100-125 Caribou) populations were the best studied, the first one due to its precarious status, and the second because it was recently reintroduced. More details on known populations are provided in Audet (1979), Courtois et al. (2001*), and de Bellefeuille (2001*).

Current Distribution According to Presence Indices

Information derived from sport hunting, large mammal surveys and chance observations show that the Caribou distribution has not changed drastically since 1972 (Figure 2a). Barren-Ground Caribou ecotype is found north of the 52nd parallel. With the exception of the Charlevoix (47° 48' N, 70° 49' W), Val-d'Or and La Sarre (48° 46' N, 79° 07' W) isolated populations, the Forest-Dwelling ecotype is found exclusively between the 49th and 55th parallels whereas the Gaspésie Mountain ecotype is the only population south of the St. Lawrence River. The main difference from the 1972 survey is the near absence of Caribou in the eastern part of the province, south of Labrador.

The 90% kernels revealed two important zones of continuous distribution (Figure 2b). The first (255 138 km^2), oriented on a north-east axis in northern Quebec, corresponds to the area frequented by the Barren-Ground Caribou during fall and winter. The second important 90% kernel (234 538 km^2), also oriented on a north-east axis and located between the Saguenay fjord and Labrador, corresponds to the area mainly used by the Forest-Dwelling Caribou. Other 90% kernels identify isolated populations: the Gaspésie Mountain population, and the Forest-Dwelling populations of Charlevoix, Val-d'Or and La Sarre, as well as two groups east of James Bay. The latter two, identified in 1991 (Anonymous 1992*), correspond either to the Rupert Forest-Dwelling population identified by Brassard (1972*) or to subsets of the George River or Leaf River Barren-Ground populations.

The 70% kernels (zones of intensive use) cover 115 282 km^2 and delimit three main areas in the north and three others in central Quebec. The three northern 70% kernels probably correspond to sub-groups of the George River population, exploited at different annual and seasonal periods. The western kernel is located in the region of the LG-4 hydroelectric dam, the second corresponds to the location of the George River population as identified by Pichette and Beau-

TABLE 1. Percentage of the zones of intensive use and the zones of continuous distribution of Caribou by ecological zone (in bold) and sub-zone (italics). The extent of intensive use and continuous distribution zones was determined using presence indices obtained from harvest, aerial surveys, scientific research and chance observations of Caribou. See Figure 2 for location of the zones of intensive use. The ecological classification follows Anonymous (2000*).

	Zones of intensive use (70% kernels)							Zones of continuous distribution (90% kernels)					
	NT – *MF*[a]	**B** – *BF*[b]	**B** – T[c]	**B** – *FT*[d]	**A** – *LA*[e]	km²		**NT** – *MF*	**B** – *BF*	**B** – *T*	**B** – *FT*	**A** – *LA*	km²
Barren-Ground population (George River)													
LG-4	–	–	100.0	–	–	7497							
Koksoak	–	–	66.9	33.1	–	31 770	]*	–	–	46.4	48.3	5.3	255 138
George River	–	–	12.9	77.3	9.8	11 579							
Mountain population													
Gaspésie	–	–	–	–	–	–		17.2	82.8	–	–	–	6 818
Forest-Dwelling populations													
Charlevoix	4.3	95.7	–	–	–	1639		20.8	79.2	–	–	–	10 954
Val-d'Or	–	100.0	–	–	–	135		37.3	62.7	–	–	–	13 849
La Sarre	–	–	–	–	–	–		–	100.0	–	–	–	8 463
Eastern James Bay	–	–	–	–	–	–		–	99.1	0.9	–	–	12 238
Manouane-Manicouagan	–	100.0	–	–	–	39 979	]*	0.5	85.5	14.0	–	–	171 040
Petit Lac Manicouagan	–	67.4	32.6	–	–	14 795							
Magpie	–	100.0	–	–	–	7888		–	93.0	7.0	–	–	17 994

[a] **Northern temperate** – *mixedwood forest*: forest of northern hardwoods and conifers (bioclimatic domain of balsam fir – yellow birch forest).
[b] **Boreal** – *boreal forest*: continuous forest, dominated by relatively dense formations of boreal coniferous or shade intolerant hardwood species (bioclimatic domain of balsam fir–white birch forest and spruce–moss forest).
[c] **Boreal** – *taiga*: open coniferous forest with lichen mat (bioclimatic domain of spruce–lichen forest).
[d] **Boreal** – *forest-tundra*: mosaic of forest of varying density and tundra dominated by shrubs and lichens (bioclimatic domain of forest tundra).
[e] **Arctic** – *low arctic*: absence of trees, presence of continuous permafrost, tundra vegetation dominated by shrubs, herbaceous species, grass-like plants, mosses and lichens (bioclimatic domain of shrub arctic tundra).
*The zones of continuous distribution of these groups overlapped; no specific data were available.

chemin (1973*), near the Koksoak River, while the eastern kernel coincides with the site identified by Bergerud (1967), at the source of the George River. The first southern 70% kernel, north of the Saguenay, corresponds to the Manouane-Manicouagan populations, identified as scattered Caribou by Brassard (1972*). The second southern kernel, northeast of the first, likely corresponds to the Petit Lac Manicouagan population, hunted in fall in the 1970s and 1980s, but also in winter concurrently with Barren-Ground Caribou since the early 1990s. The kernel south of Labrador represents the Magpie River population (also called the Lac Joseph population).

Nearly all the areas of the zones of continuous use and the zones of intensive use were located in the boreal ecological zone (Table 1). The extent of the ecological sub-zones differed among kernels, but the boreal forest and the taiga dominated, except for the Barren-Ground ecotype which used the forest tundra and the taiga equally. The populations in Gaspésie, Charlevoix and Val-d'Or were the only ones located at the edge of the mixedwood forest.

Forest fire cycle maps (Gauthier et al. 2001) indicated that most Caribou observations were made in areas with long fire cycles (Table 2). The zones of continuous distribution were dominated by long or very long fire cycles (200-500 years: 77.8% of the area; 100-200 years: 5.8%; <100 years: 16.4%), and 95.7% of the zones of intensive use were located in sites having fire cycles of 200-500 years. Forest fire cycles were not available for the Barren-Ground Caribou kernels but Payette et al. (1989) reported very long fire cycles (> 7800 years) in the forest tundra and the taiga.

Change in Harvest Characteristics Since 1971

Over the last 30 years, Caribou hunting has been permitted in the hunting zones where the six main 70% kernels were located (Table 3). Total harvest and harvest per unit area were particularly high in the three kernels of the Barren-Ground populations but also in the Magpie and Petit Lac Manicouagan populations. In contrast to Caribou, Moose harvest per unit area decreased from south to north.

Trends in harvest differed between kernels (Figure 3). A significant drop was noted in the George River 70% kernel. This decrease was compensated by an increase of the same magnitude in the Koksoak kernel in the mid-1980s, and later in the LG-4 kernel. In the Manouane-Manicouagan, Petit Lac Manicouagan and Magpie populations, the fall harvest decreased slightly or drastically during the 1970s or the 1980s.

Winter hunting was permitted in the Petit Lac Manicouagan kernel and in the northern populations. In northern Quebec, the fall and winter harvests for each kernel showed a similar trend, probably because the same populations were exploited during the two hunting seasons. For Petit Lac Manicouagan, the harvest was about 50 times higher in winter than in fall. The winter season was instituted in order to harvest the

TABLE 2. Percentage of the area of the zones of intensive use and the zones of continuous distribution of Caribou according to length of fire cycle. The extent of the zones was determined using presence indices obtained from harvest, aerial surveys, scientific research and chance observations of Caribou.

	Zones of intensive use (70% kernels)					Zones of continuous distribution (90% kernels)				
	n.d.[1]	< 100 years	100-200 years	200-500 years		n.d.	< 100 years	100-200 years	200-500 years	
Mountain population										
Gaspésie	–	–	–	–		17.2	–	–	82.8	
Forest-Dwelling populations										
Charlevoix	4.3	–	–	95.7		14.0	–	–	86.0	
Val-d'Or	–	–	100.0	–		36.9	–	63.1	–	
La Sarre	–	–	–	–		–	–	100.0	–	
Eastern James Bay	–	–	–	–		60.4	39.6	–	–	
Manouane-Manicouagan	–	4.4	–	95.6	*	48.3	9.2	0.1	42.3	
Petit Lac Manicouagan	100.0	–	–	–						
Magpie	100.0	–	–	–						

[1] No data available.
*The zones of continuous distribution of these groups overlapped; no specific data were available

TABLE 3. Mean annual Caribou harvest (± standard error [*n* = number of years]), and Caribou and Moose annual harvest per surface area between 1971 and 1999 in the zones of intensive use (70% kernels) where hunting was permitted[a].

	Caribou harvest		Harvest / 100 km^2	
	Fall	Winter	Caribou	Moose
Barren-Ground population				
George River				
LG-4	842 ± 402.8 (8)	2037.4 ± 579.9 (11)	34.96 ± 10.80 (11)	0.03 ± <0.01 (9)
Koksoak	1240.7 ± 228.1 (27)	1042.4 ± 190.5 (24)	7.03 ± 1.25 (27)	<0.01 ± - (1)
George River	574.9 ± 81.4 (28)	264.1 ± 25.0 (25)	6.98 ± 0.86 (28)	0.01 ± <0.01 (2)
Forest-Dwelling populations	–	–	–	–
Manouane-Manicouagan	22.2 ± 2.4 (28)	–	0.06 ± 0.01 (28)	0.45 ± 0.03 (29)
Petit Lac Manicouagan	10.7 ± 1.3 (27)	384.4 ± 108.4 (15)	1.52 ± 0.47 (27)	0.16 ± 0.01 (29)
Magpie	84.3 ± 72.0 (16)	53.4 ± 24.5 (10)	1.33 ± 0.81 (18)	0.21 ± 0.02 (29)

[a] No data are available for the Mountain populations; hunting of the Gaspésie population has not been allowed since 1929 (Moisan 1956), and the Torngat Mountain population was not identified by a 70% kernel, because the harvest was either too low or undocumented.

Barren-Ground Caribou during its southern migration. The high winter harvest suggests that the flux from the George River population was important at the start of the 1990s. In the absence of important changes in hunting effort, the decline in winter harvest after 1992 suggests that the Barren-Ground Caribou did not migrate far enough south to reach the Petit Lac Manicouagan area.

The structure of the harvest also differed between kernels. In northern Quebec, an increase in productivity was noted up until the mid-1980s, at least in the George River kernel, but then underwent a significant decrease (Figure 4). The number of males per 100 females diminished in the George River kernel, whereas it increased in the Koksoak and the LG-4 kernels suggesting that hunters were more selective probably due to a population increase in these areas (Figure 5). The percentage of calves and the number of males per 100 females varied from year to year in the southern populations without conclusive explanation.

The fall harvest of Caribou between 1971 and 1999 was negatively correlated to the Moose harvest in the LG-4 kernel, positively correlated in the Manouane-Manicouagan population, whereas these two variables appeared to be independent in other kernels (Table 4). The temporal change in Caribou harvest was positively correlated to the number of males and calves per 100 females as well as to the percentage of calves in two of the six kernels examined.

Discussion

Caribou populations seem to have undergone significant growth on a worldwide scale during the 1980s (Bergerud 1988). However, this increase has been mainly due to the Barren-Ground populations, estimated at about 3 000 000 Caribou in the mid-1980s, that is, practically double the numbers estimated a decade earlier. During the same period, the Forest-Dwelling populations barely comprised 325 000 individuals and appeared to have undergone notable but inaccurately quantified decreases (Bergerud 1988; Cumming 1992; Mallory and Hillis 1998). However, some authors express reservations as to the magnitude of the changes due to the inaccuracy of historical information (Bradshaw and Hebert 1996).

Historical Distribution

There is no doubt as to an historical reduction in the Caribou distribution in Quebec. Except for the Gaspésie population, the species is no longer present south of the St. Lawrence River, where it was frequently sighted until about 1875 (Martin 1980; Guay 1983). However, its precise historical distribution and abundance in the St. Lawrence valley are not known. This area is at present dominated by hardwood and mixedwood forest, unsuitable for Caribou. Mature hardwoods also dominated the forest landscape in the early 19th century (Richard 1993), which indicates that Caribou were probably not abundant southwest of

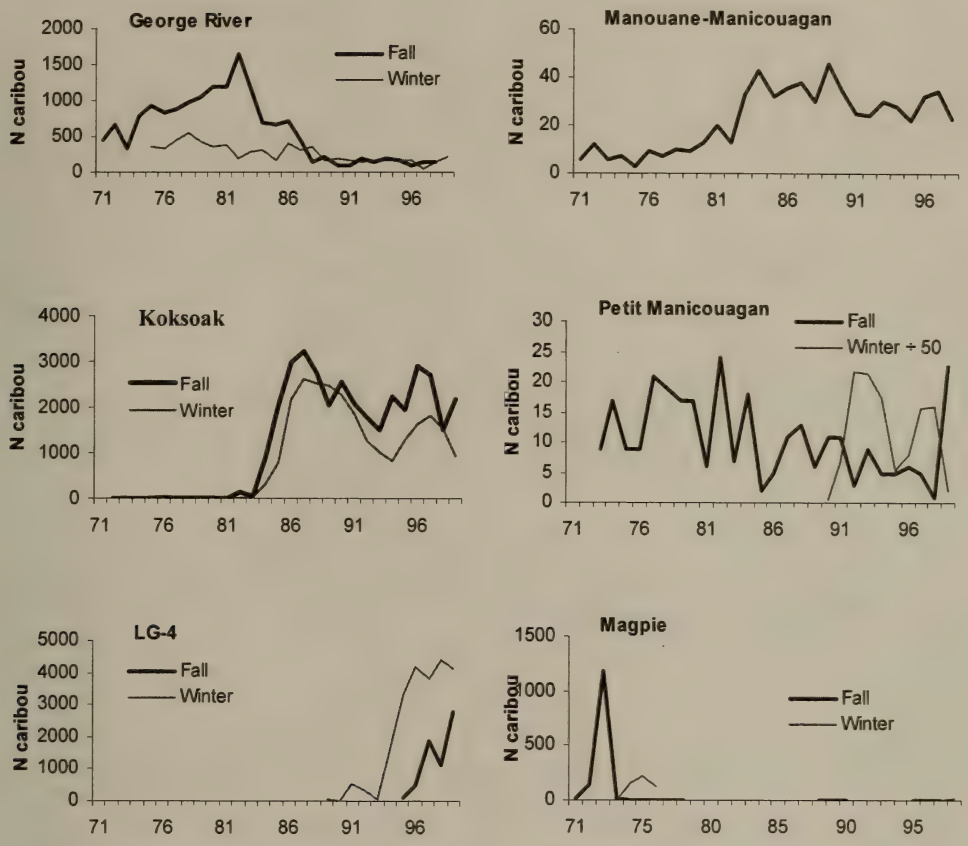


FIGURE 3. Harvest of Caribou in the zones of intensive use (70% kernels) where hunting was allowed between 1971 and 1999.

Quebec City, even at that time. Its distribution was probably limited to sites dominated by coniferous trees.

The main direct causes of the Caribou decline appear to have been overharvesting and predation, and in some cases, the transmission of the Meningeal Worm (*Parelaphostrongylus tenuis*) by White-tailed Deer (*Odocoileus virginianus*) (Bergerud 1974, 1988; Martin 1980; Bergerud and Mercer 1989; Jolicoeur 1993*). In addition, the development of agriculture and forestry probably led to growth in Moose and deer populations due to conversion of conifer stands to deciduous and mixed stands, which may have favoured an increase in Wolf abundance and, consequently, predation on Caribou (Bergerud 1974; St-Vincent 1981*; Bellehumeur et al. 1985*; Gingras et al. 1989; Jolicoeur 1993*). These habitat modifications may also have favoured the growth of Black Bear (*Ursus americanus*) populations and predation on Caribou calves. There is mounting evidence that habitat changes and increased predation contribute to the decline of Woodland Caribou (Bergerud and Elliot 1986; Seip 1992; Seip and Cichowski 1996).

The effect of any particular cause is difficult to quantify, since habitat changes that led to expansions in Moose, deer and Wolf populations occurred at a time when hunting was very intense. Nevertheless, Caribou disappeared from the southern part of its distribution range simultaneously all across North America. To explain this situation, Bergerud (1974) examined (1) changes in the availability of lichens due to forest fires and logging, (2) the impact of hunting and predation, (3) the combined effects of the availability of lichens and predation, and finally, (4) the simultaneous impact of social pressures (following population growth) and predation. According to Bergerud (1974), only the second hypothesis seemed probable. Caribou can use open habitats and often take traditional routes when travelling; they live in groups, and are not fearful, making them very vulnerable to hunting. Although there may not necessarily be a cause and effect relationship, stories about excessive hunting abound and the disappearance of the Caribou coincides with the arrival of the repeating rifle (St. Cyr 1873; Moisan 1956; Martin 1980; Guay 1983;

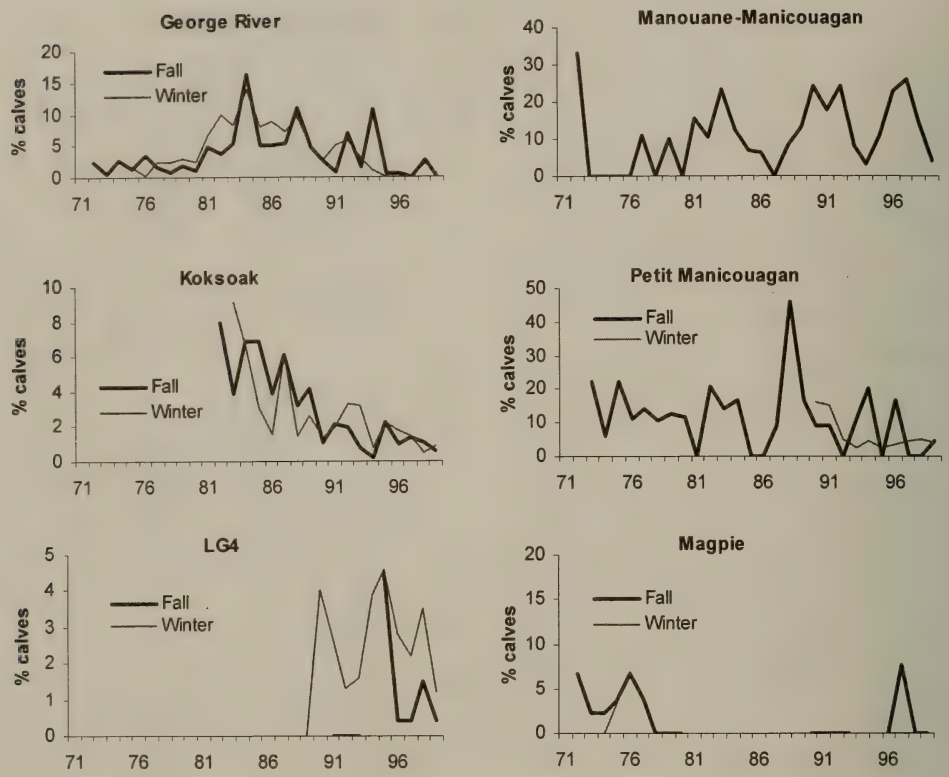


FIGURE 4. Percentage of calves in Caribou harvest in the zones of intensive use (70% kernels) where hunting was allowed between 1971 and 1999.

Jolicoeur 1993*). The impact of limiting factors is exacerbated by the low productivity of Caribou, with females giving birth to only one calf per year.

Current Distribution

In western Quebec, Caribou has been virtually absent south of the 50th parallel and west of the 78th meridian for at least 50 years. A 1968 survey covering northern Abitibi (74°00'-79°30' W, 48°00'-50°00' N) noted only six Caribou track networks over 92 715 km^2 and no mention was made of any previous observations (Anonymous 1968*). Moreover, Caribou presence was not reported in surveys carried out southwest of this area (Vallée and Poitras 1973*). A few isolated populations have been known since the 1950s, because Seton (1953) marvelled at the absence of antlers in many females in northwestern Quebec. Brassard (1968*) identified the Val-d'Or population without mentioning its abundance, obviously because he observed only a few individuals. Several surveys conducted during the 1970s revealed the presence of a few individuals in Val-d'Or and near the Ottawa River (47° 52' N, 78° 26' W, between Rapide-Sept and Rapide-Deux, perhaps individuals from the Val-d'Or population), and chance observations were reported near Val-Paradis (La Sarre population) and Matagami (49° 46' N, 77° 40; probably individuals from the Rupert population) (St-Vincent 1981*). These populations appear to have been the only ones totally or partially located south of the 50th parallel, west of the Charlevoix region.

Data available for the east-central part of the province have suggested low but relatively stable densities since the early 1980s. The distribution of Caribou on the North Shore was re-evaluated in 1982 using 120 60-km^2 sample plots (Brassard 1982*). The total population was not estimated, but the presence of Caribou track networks was noted in 41% of the plots. In 1988, Caribou were present in 33 of the 84 (40%) plots surveyed west of Natashquan on the North Shore and in the Saguenay region (Gingras et al. 1989*). In 1991, 12 plots out of 30 (40%) contained Caribou track networks in the western part of the North Shore.

In contrast, Caribou appeared to be rare farther east. In 1993, Bourbonnais et al. (1997*) observed Caribou in only seven (20%) of the 60 plots surveyed in the Natashquan region. Still farther east, only one (6%) of

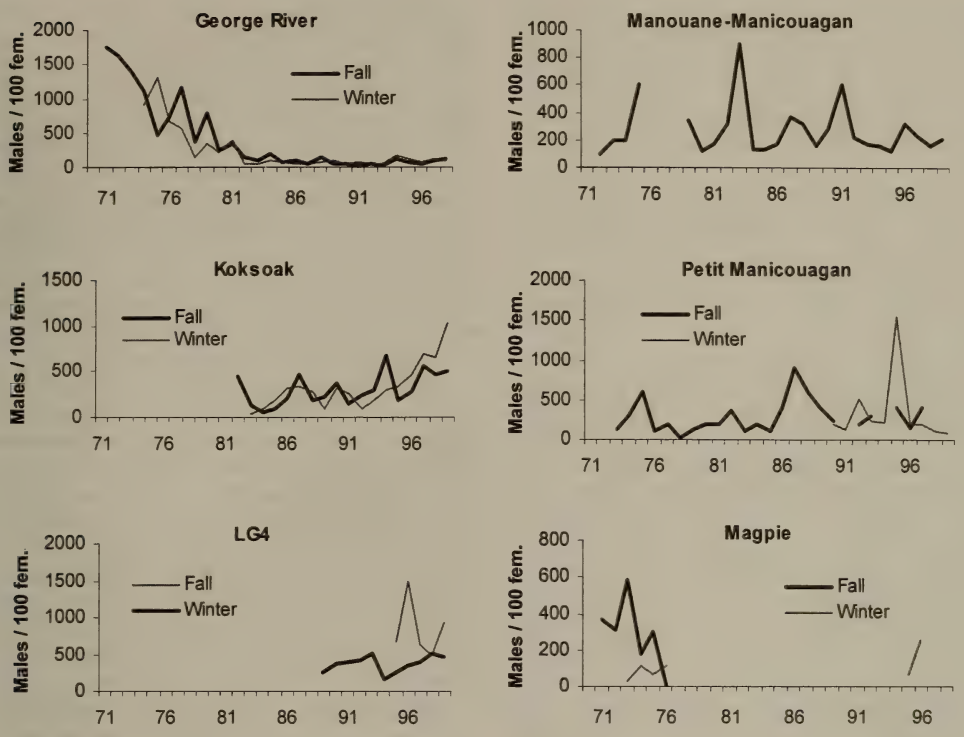


FIGURE 5. Number of males per 100 females in Caribou harvest in the zones of intensive use (70% kernels) where hunting was allowed between 1971 and 1999.

the 18 sample plots covered in 1983 contained Caribou (Barnard 1983*). According to available data, the Saint-Augustin population seems very reduced or extirpated, although the Native people hunt an indeterminate number of Caribou. However, the dearth of information available for this relatively inaccessible and uninhabited region should be kept in mind. No sport hunting has been allowed in that area since 1979, and it has not been surveyed for almost 20 years.

The range probably shrank between the 1960s and 1980s in the eastern part of the North Shore. However, the major change that has come about south of the 52nd parallel since the late 1950s is undoubtedly the disappearance of large Forest-Dwelling populations that frequented the North Shore and southern Labrador. The magnitude of the changes cannot be accurately quantified due to the imprecision of the first surveys, the absence of recent inventories, and changes in the areas flown and the methods used. However, the decline itself is not in doubt. Desmeules and Brassard (1963*) estimated that there were 9774 Caribou on the North Shore, within an 80-km wide strip, between Sept-Îles (50° 13' N, 66° 23' W) and Saint-Augustin (51° 13' N, 58° 40' W). Brassard and Bouchard (1968*) evaluated the population at 5629 individuals within an even larger area than in 1963. In 1972, the population was estimated at 7500 Caribou for the entire North Shore south of the 51st parallel (Brassard 1972*). In 1978, it was estimated at 13 158 ± 6 590 individuals south of the 53rd parallel (Audet 1979*). Based on surveys of large blocks carried out in the 1990s, density could be of the order of 0.97 to 1.6 Caribou per 100 km^2 (Gingras and Malouin 1993*; Bourbonnais et al. 1997*; Maltais 1997*). Assuming that no large population has been missed and that the zones of continuous distribution provide a reasonable estimate of the area currently occupied, there would be between 1900 and 3200 Forest-Dwelling Caribou north of the Saguenay fjord.

The most frequently cited causes of decline are excessive hunting, predation and insufficient recruitment (Bergerud 1967; Audet 1979*; Cinq-Mars 1977*; Folinsbee 1979). Hunting is probably the main cause. Bergerud (1967) estimated the harvest rates to be from 26-27% between 1958 and 1963 in the Mealy Mountain population, south of Labrador. Taking into account losses from natural causes, the total mortality rate was 31% per year, whereas the recruitment was barely 11%. The Saint-Augustin population, adjacent to and perhaps an extension of the Mealy Mountain population,

TABLE 4. Correlation between fall harvests of Caribou on the one hand, and Moose harvest, males / 100 females, calves / 100 females and % calves in Caribou harvest on the other hand in the zones of intensive use (70% kernels) between 1971 and 1999.

Zone of intensive use	Spearman r (P)[a]							
	Moose harvest		Males / 100 females		Calves / 100 females		% calves	
Barren-Ground population								
George River								
LG-4	–0.64	(0.01)	0.20	(0.70)	–0.03	(0.95)	0.60	(0.11)
Koksoak	–0.15	(0.45)	0.39	(0.10)	–0.18	(0.45)	0.26	(0.89)
George River	0.00	(0.99)	0.58	(<0.01)	0.56	(<0.01)	0.26	(0.18)
Forest-Dwelling populations	–		–		–		–	
Manouane-Manicouagan	0.85	(< 0.01)	–0.03	(0.87)	0.15	(0.47)	0.31	(0.11)
Petit Lac Manicouagan	0.14	(0.44)	–0.14	(0.52)	0.47	(0.02)	0.43	(0.02)
Magpie	0.11	(0.57)	0.68	(0.05)	0.43	(0.23)	0.79	(< 0.01)

[a] $14 \leq n \leq 29$.

probably experienced a similar fate (Brassard 1972*). The Magpie River population, exploited simultaneously in Quebec and in Labrador, comprised about 5000 Caribou in the mid-1960s but only 1300 to 3000 by the mid-1970s. According to Folinsbee (1976*, 1979), this population appeared to have been overexploited. At that time, subsistence hunting took at least 176 to 254 Caribou per winter, to which natural mortality (≈ 150), sport hunting (≈ 120) and illegal or undeclared hunting should be added. Annual harvest reported in our files varied between 128 and 1162 Caribou in the 70% kernel of the Magpie River between 1973 and 1977, meaning that the harvest rates exceeded 30% at that time.

It is not entirely impossible that the large populations have migrated into other sectors. Several surveys in the 1960s and 1970s showed population movements of many tens of kilometres. However, if such was the case, these groups would have been located during subsequent surveys of Moose and Caribou, but this has not occurred over the last two decades. Caribou are philopatric, and as observed at present in northern Quebec, site changes occur when densities increase, not when they decline (Bergerud 1974). One might also think that the large populations observed on the North Shore in the 1960s could have been extensions of migratory populations from northern Quebec. However, published survey maps show that the northern populations were located farther north, that they only started to increase in abundance in the 1950s, and that their distribution range did not expand considerably before the 1980s (Banfield and Tener 1958; Bergerud 1967; Pichette and Beauchemin 1973*; Messier et al. 1988). Even today, the distribution of Barren-Ground Caribou does not extend south of the 52nd parallel (Schaefer et al. 1999).

Causes of Temporal Changes in Barren-Ground Caribou

The negative correlation noted between Caribou and Moose harvests in kernel LG-4 is probably accidental (Table 4). In northern Quebec, the density of Moose (< 0.3 per 10 km^2; Maltais et al. 1993*) is probably too low to influence Wolf abundance, since 2.0 Moose/ 10 km^2 are required to support stable Wolf populations (Messier 1994). This situation is not likely to change in the future, since the habitat carrying capacity is low for Moose at this latitude, where shrubs near waterways are the only sites of interest for this species (Joyal 1987).

Within each group of northern Quebec, the fall and winter harvests had nearly identical characteristics, suggesting that the same populations are exploited during both hunting seasons. However, there were marked differences in harvest characteristics between the northern groups. The decline in the harvest in the George River kernel indicates that Caribou numbers have been diminishing at this location since the mid-1980s. If the migratory behaviour of males had not

changed, the decrease in the proportion of males in the harvest could suggest a reduction in the selectivity of hunters as a result of an increasingly difficult hunt. The decline could be attributed to a lower population productivity, as suggested by the structure of the sport harvest (Figure 4).

Changes in the abundance of the George River population are in line with the observations of Morneau and Payette (1998). Based on the scars left on tree roots by the passage of Caribou, these authors consider that the species was rare during the 1940s and 1950s in the George River region. The abundance increased in the early 1970s, reached a maximum between 1984 and 1989, and then declined significantly in the early 1990s. Changes in abundance suggested by Morneau and Payette (1998) corroborate population increases noted during aerial surveys conducted during the 1970s and the 1980s (Couturier et al. 1996). Telemetry data and computer simulations realized by Crête et al. (1996) suggest a slight decline in populations after 1986 which seems to concur with the observations of Morneau and Payette (1998) but to contradict the 1993 aerial survey and demographic data which suggest a reduction in the rate of increase rather than a decline (Couturier et al. 1996; Messier et al. 1988). Considering the limits of simulations models, we cannot exclude that the scars left on tree roots could have diminished due to a change in migration routes. The increased harvest in the Koksoak River and LG-4 reservoir region following the decline in the George River area support this hypothesis. Moreover, the increased representation of males in the harvest of Koksoak and LG-4 suggests a greater selectivity on the part of hunters following an increase in Caribou abundance. In the early 1980s, Brown et al. (1986) observed large groups of Caribou at the Caniapiscau reservoir, south-west of the George River and presumably belonging to the George River population. In the early 1990s, a few large groups of Caribou, probably migrators from George River or Leaf River, were also observed in west-central Québec, around the 51st parallel (Anonymous 1992*).

Causes of Temporal Changes in Forest-Dwelling Caribou

The groups of Caribou identified do not constitute a homogeneous population. Hunting statistics show regional differences in terms of population density, structure and temporal changes. For example, the Magpie population produced large harvests for a few years, and then practically disappeared in the mid-1970s, well before hunting was closed in 1979. In the mid-1970s, the Manouane-Manicouagan population, located a few hundred kilometres farther west, provided a small harvest, which increased up until the 1980s even though the harvest was subject to quotas. The harvest in Petit Lac Manicouagan, located to the northeast of Manouane-Manicouagan, showed intermediate trends. The fall harvest declined in a nearly constant fashion, which may have been caused by a reduction in the number of hunting permits during that season. However, a considerable increase in the winter harvest was noted between 1990 and 1995, but was followed by a sharp decrease. These changes can probably be attributed to the irregular migrations of the Barren-Ground Caribou, which are the focus of the winter hunt, and which account for most of the harvest in this sector. Nevertheless, the downward trend in the fall harvest could indicate a decline in the abundance of Forest-Dwelling Caribou, perhaps partly caused by incidental kills of that ecotype during the winter hunt of Barren-Ground Caribou.

We were expecting an increase in the Moose harvest at sites where the Caribou harvest had declined, which would have suggested an increase in predation following population growth in Moose and Wolf. This may have occurred south of the 49th parallel at the end of the 19th century (St. Cyr 1873; Gingras et al. 1989; Jolicoeur 1993*). However, this hypothesis does not seem to be supported by harvest data collected during the last three decades. For example, Moose and Caribou harvests were positively correlated in the Manouane-Manicouagan population, implying that the annual variations were more tightly linked to changes in hunting pressure, since the harvest of both species is carried out simultaneously in that area. In the Petit Lac Manicouagan and Magpie populations, harvests of Caribou and Moose evolved independently and Caribou declines followed very large harvests. In the studied populations, forest disturbance was probably not large enough to significantly increase the importance of early successional forests and provoke an increase of Moose and Wolf abundance that would have favoured Caribou predation. Instead, our results suggest that declines in the Forest-Dwelling Caribou populations may have been mainly caused by excessive hunting, as previously proposed (Bergerud 1967; Folinsbee 1979; Cinq-Mars 1977*).

A considerable increase in the Caribou harvest can be noted from south to north, due to the presence of the large Barren-Ground populations in the North. In winter, they could migrate as far south as the Petit Lac Manicouagan kernel. At this location, the characteristics of the fall and winter harvests differ considerably in terms of abundance and structure, suggesting the presence of different populations in both seasons. The winter harvest seems to be supported mainly by migratory populations since the decline in the harvest and the percentage of calves is similar to that noted for the George River population. The Forest-Dwelling Caribou populations farther south do not seem to be influenced directly by the migratory animals.

Conclusion

In Quebec, the range of Caribou has decreased considerably over the last 150 years. The disappearance of Caribou has usually been associated with excessive hunting as well as with the arrival of Moose and

Wolves following logging (Martin 1980; Bellehumeur et al. 1985*; Jolicoeur 1993*). Northern populations recovered, beginning in the mid-1950s, but the Mountain population in Gaspésie and the Forest-Dwelling populations have continued to decline. The decline of the Gaspésie population appears to be due to hunting in the early 20th century (Moisan 1957) and predation since the early 1970s (Crête and Desrosiers 1995). The decrease in Forest-Dwelling Caribou, which was particularly rapid until the mid-1970s, seems to be the result of excessive hunting in eastern Quebec. Sport hunting of Forest-Dwelling Caribou was subject to a quota in 1979 and has been banned since winter 2001, but subsistence hunting continues. At the present time, it is difficult to predict the population trend in a context where access to the northern forests is increasing and early successional forests are developing due to logging. Moreover, despite the fact that we did not detect any relationships between Moose and Caribou abundance, it would be premature to conclude that habitat changes have no influence on Caribou. The precision of historical data is relatively low, so a type II error cannot be ruled out. Falsely concluding that no decline is occurring would be a more serious error in biological conservation than falsely concluding that a decline is occurring (Caughley and Gunn 1996).

The real situation of the Forest-Dwelling Caribou and their future trend remain speculative due to the lack of recent surveys. Unfortunately, an aerial survey programme would require a large investment due to the low densities and the contiguous distribution of Forest-Dwelling Caribou. To limit the costs, priority should be given to surveying the zones of intensive use.

Acknowledgments

The authors are indebted to Pierre Drapeau, James Schaefer, François Potvin and two anonymous referees who commented on an earlier version of this paper. This study would not have been possible without the contribution of the authors of the publications and documents consulted. We appreciated their clear-sightedness, and particularly admire the audacity and bravery they required to carry out the first aerial surveys, at a time when northern travel was often still done by means of dogsled. We also thank those who graciously reported their Caribou observations and those who set up systems for collecting this information. We wish to underscore the contribution of Daniel Banville, Mario Duchesne and Marcel Paré, among others.

Documents Cited

Audet, R. 1979*. Inventaire aérien de l'ensemble du bassin versant de la moyenne et de la basse Côte-Nord. Hydro-Québec, Direction de l'Environnement. Montréal, Québec. 42 pages.

Anonymous. 1968*. Inventaire aérien des ongulés sauvages, section située dans la nord de l'Abitibi (janvier 1968). Service de la faune. Québec, Québec. 7 pages.

Anonymous. 1992*. Complexe Nottaway-Broadback-Rupert : Les mammifères – volume 3 – Abondance et habitat du caribou (*Rangifer tarandus*). Hydro-Québec, vice-présidence Environnement. Le Groupe Boréal. St-Romuald, Québec. 55 pages + appendix.

Anonymous. 2000*. Cartographie numérique des niveaux supérieurs du système hiérarchique de cartographie écologique du Ministère des Ressources naturelles du Québec et banque de données descriptives des districts écologiques. Ministère des Ressources naturelles. Québec, Québec.

Barnard, F. 1983*. Rapport de l'inventaire aérien des ongulés de la basse Côte-Nord en février 1983. Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale de la Côte-Nord. Sept-Îles, Québec. 11 pages.

Bellehumeur, P., C. Brassard, and **A. Lachappelle.** 1985*. Répartition et habitat du caribou de la région de Val-d'Or. Perspective d'avenir. Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale de l'Abitibi-Témiscamingue. Rouyn-Noranda, Québec. 50 pages.

Bourbonnais, N., A. Gingras, and **B. Rochette.** 1997*. Inventaire aérien du caribou dans une portion de la zone de chasse 19 sud (partie est) en mars 1993. Ministère de l'Environnement et de la Faune, Direction régionale de la Côte-Nord. Sept-Îles, Québec. 24 pages.

Brassard, J.-M. 1967*. Inventaire aérien des ongulés sauvages de la Côte-Nord et identification des aires d'hivernement en fonction des formes du relief et de la végétation. Service de la faune. Québec, Québec. 15 pages.

Brassard, J.-M. 1968*. La distribution des ongulés sauvages de la province de Québec. Ministère du Tourisme, de la Chasse et de la Pêche, Service de la faune. Québec, Québec. 8 pages.

Brassard, J.-M. 1972*. Inventaire aérien du gros gibier. Ministère du Tourisme, de la Chasse et de la Pêche, Service de la faune. Québec, Québec. 39 pages.

Brassard, J.-M. 1982*. Inventaire aérien du caribou des territoires situés sur les versants de la Côte-Nord du Saint-Laurent. Ministère du Tourisme, de la Chasse et de la Pêche, Service de la faune. Québec, Québec. 13 pages.

Brassard, J.-M., and **R. Bouchard.** 1968*. Révision des inventaires aériens de l'orignal faits en 1964 et 1965 (janvier 1968). Ministère du Tourisme, de la Chasse et de la Pêche, Service de la faune. Québec, Québec. 15 pages.

Cinq-Mars, J. 1977*. Inventaire aérien du caribou sur la Basse-Côte-Nord, hiver 1977. Ministère du Tourisme, de la Chasse et de la Pêche, Direction régionale de la Côte-Nord. Sept-Îles, Québec. 15 pages.

Courtois, R., J.-P. Ouellet, A. Gingras, C. Dussault, L. Breton, and **J. Maltais.** 2001*. Changements historiques et répartition actuelle du caribou au Québec. Société de la faune et des parcs. Québec, Québec. 46 pages.

de Bellefeuille, S. 2001*. Le caribou forestier et la sylviculture: revue de littérature et synthèse de la recherche et de l'aménagement en cours au Québec. Ministère des Ressources naturelles. Direction de l'environnement forestier. Québec, Québec. 86 pages.

DesMeules, P., and **J.-M. Brassard.** 1963*. Inventaire préliminaire du caribou, *Rangifer tarandus*, d'un secteur de la Côte-Nord et du secteur centre de l'Ungava. Ministère du Tourisme, de la Chasse et de la Pêche, Service de la faune. Québec, Québec. 40 pages.

Folinsbee, J. D. 1976*. Lac Joseph caribou – Wintering aerial survey, January 1976. Department of Tourism, Wildlife Division, Project 75C-39. St. John's, Newfoundland. 4 pages + appendix.

Gingras, A., R. Audy, and **R. Courtois.** 1989*. Inventaire aérien de l'orignal dans la zone de chasse 19 à l'hiver 1987-88. Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale de la Côte-Nord. Sept-Îles, Québec. 58 pages.

Gingras, A., and **B. Malouin.** 1993*. Inventaire aérien du caribou dans la zone de chasse 19 sud (partie ouest) en mars 1991. Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale de la Côte-Nord. Sept-Îles, Québec. 26 pages.

Jolicoeur, H. 1993*. Des caribous et des hommes. L'histoire de la réintroduction du caribou dans les Grands-Jardins. Ministère du Loisir, de la Chasse et de la Pêche, Direction de la faune et des habitats. Québec, Québec. 76 pages.

Joly, R., and **J.-M. Brassard.** 1980*. Inventaire aérien des ongulés d'une portion sud du territoire de la municipalité de la Baie-James. Ministère du Loisir, de la Chasse et de la Pêche, Direction générale de la faune, Rapport DGF 16: 119-136.

Le Hénaff, D. 1976a*. Vérification des principales aires du caribou (*Rangifer tarandus*) dans le secteur de Waco (basse Côte-Nord) et au Nouveau-Québec, avril 1976. Ministère du Tourisme, de la Chasse et de la Pêche. Service de la recherche biologique. Québec, Québec. 31 pages.

Le Hénaff, D. 1976b*. Inventaire aérien du secteur Natashquan à Blanc-Sablon. Ministère du Tourisme, de la Chasse et de la Pêche, Service de la faune. Québec, Québec 7 pages.

Maltais, J. 1997*. Inventaire de reconnaissance (aire commune 24-1) : caribous des bois (*Rangifer tarandus*) de la région des lacs Péribonca et Manouane. Abondance et besoins de l'espèce par rapport à l'exploitation forestière. Stone-Consolidated Inc., Division Saguenay. Chicoutimi, Québec. 39 pages + appendix.

Maltais, J., Y. Leblanc, and **S. Couturier.** 1993*. Inventaire aérien de l'orignal dans la zone de chasse 22 en février et mars 1991. Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale du Nouveau-Québec. Chibougamau, Québec. 39 pages.

Paquet, M. 1997*. Toward a mountain caribou management strategy for British Columbia. British Columbia Environment, Wildlife Branch. 72 pages.

Paré, M., and **C. Brassard.** 1994*. Écologie et plan de protection de la population de caribous de Val-d'Or. Ministère de l'Environnement et de la Faune, Direction régionale de l'Abitibi-Témiscamingue. Rouyn-Noranda, Québec. 56 pages.

Pichette, C., and **P. Beauchemin.** 1973*. Inventaire aérien du caribou. Ministère du Tourisme, de la Chasse et de la Pêche. Service de la faune. Québec, Québec. 11 pages.

Sebbane, A., and **R. Courtois.** 2001*. Restructuration du Système d'Information de la Grande Faune. Société de la faune et des parcs du Québec, Direction de la recherche sur la faune. Québec, Québec. 21 pages + appendix.

St-Vincent, P. 1981*. Le caribou (*Rangifer tarandus*) en Abitibi-Témiscamingue. Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale de l'Abitibi-Témiscamingue. Rouyn-Noranda, Québec. 32 pages.

Vallée, J., and **C. Poitras.** 1973*. Inventaire des cervidés dans le secteur sud de la Mauricie. Ministère du Tourisme, de la Chasse et de la Pêche. Service de la faune. Trois-Rivières, Québec. 8 pages.

Literature Cited

Audet, R. 1979. Histoire du caribou du Québec-Labrador et évolution des populations. Recherches amérindiennes au Québec 9: 17-28.

Anonymous. 1996. Arc View GIS. The geographic system for everyone. Environmental System Research Institute Inc., Redlands, California, USA.

Banfield, A. W. F. 1961. A revision of the reindeer and caribou genus *Rangifer*. National Museum of Canada, Bulletin 177, Biological Series 66. Ottawa, Ontario. 137 pages.

Banfield, A. W. F., and **J. S. Tener.** 1958. A preliminary study of Ungava caribou. Journal of Mammalogy 39: 560-573.

Bergerud, A. T. 1967. Management of Labrador caribou. Journal of Wildlife Management 31: 621-635.

Bergerud, A. T. 1974. Decline of caribou in North America following settlement. Journal of Wildlife Management 38: 757-770.

Bergerud, A. T. 1988. Caribou, wolves and man. Trends in Ecology and Evolution 3: 68-72.

Bergerud, A. T., and **J. P. Elliot.** 1986. Dynamics of caribou and wolves in Northern British Columbia. Canadian Journal of Zoology 64: 1515-1529.

Bergerud, A. T., and **W. E. Mercer.** 1989. Caribou introductions in eastern North America. Wildlife Society Bulletin 17: 111-120.

Bradshaw, C. J. A., and **D. M. Hebert.** 1996. Woodland caribou population decline in Alberta: fact or fiction? Rangifer, Special Issue 9: 223-234.

Brassard, J.-M. 1979. Le caribou. L'Aubelle, Supplément au numéro 15: 9-11.

Brown, W., J. Huot, P. Lamothe, M. Paré, G. St-Martin, and **J. B. Theberge.** 1986. The distribution and movement patterns of four woodland caribou herds in Québec and Labrador. Rangifer, Special Issue 1: 43-49.

Caughley, G., and **A. Gunn.** 1996. Conservation biology in theory and practice. Blackwell Science Inc., Cambridge, Massachusetts. 459 pages.

Courtois, R., L. Bernatchez, J.-P. Ouellet, and **L. Breton.** 2003. Significance of caribou ecotypes from a genetic viewpoint. Conservation Genetics 4: 393-404.

Couturier, S., R. Courtois, H. Crépeau, L.-P. Rivest, and **S. Luttich.** 1996. The June 1993 photocensus of the Rivière George caribou herd and comparison with an independent census. Rangifer, Special Issue 9: 283-296.

Crête, M., S. Couturier, B. J. Hearn, and **T. E. Chubbs.** 1996. Relative contribution of decreased productivity and survival to recent changes in demographic trend of the Rivière George Caribou herd. Rangifer, Special Issue 9: 27-36.

Crête, M., and **A. Desrosiers.** 1995. Range expansion of coyotes, *Canis latrans*, threatens a remnant herd of caribou, *Rangifer tarandus*, in Southeastern Québec. Canadian Field-Naturalist 109: 227-235.

Crête, M., and **C. Dussault.** 1987. Using hunter statistics to estimate density, cow-calf ratio and harvest rate of moose in Quebec. Alces 23: 227-242.

Cumming, H. G. 1992. Woodland caribou: facts for forest managers. Forestry Chronicle 68: 481-491.

Cumming, H. G., and **D. B. Beange.** 1993. Survival of woodland caribou in commercial forests of northern Ontario. Forestry Chronicle 69: 579-588.

Folinsbee, J. D. 1979. Distribution et abondance passées et présentes du caribou (*Rangifer tarandus*), au Labrador méridional et dans les régions adjacentes du Québec. Recherches Amérindiennes au Québec 9: 37-46.

Gauthier, S., A. Leduc, B. Harvey, Y. Bergeron, and **P. Drapeau.** 2001. Les perturbations naturelles et la diversité écosystèmique. Naturaliste canadien 125 (3): 10-17.

Gingras, S., S. Lirette, and **C. Gilbert.** 1989. Le club Triton. Les Éditions Rapide-Blanc Inc. 300 pages.

Guay, D. 1983. Histoires vraies de la chasse au Québec. VLB Éditeur. Montréal, Québec. 268 pages.

Hooge, P. N., and **B. Eichenlaub.** 1997. Animal movement extension to Arcview. Version 1.1. Alaska Biological Science Center, U.S. Geological Survey. Anchorage, Alaska.

Joyal, R. 1987. Moose habitat investigations in Québec and management implications. Swedish Wildlife Research, Supplement 1: 139-152.

Larivière, S., H. Jolicoeur, and **M. Crête.** 2000. Status and conservation of the gray wolf (*Canis lupus*) in wildlife reserves of Québec. Biological Conservation 94: 143-151.

Mallory, F. F., and **T. L. Hillis.** 1998. Demographic characteristics of circumpolar caribou populations: ecotypes, ecological constraints/releases, and population dynamics. Rangifer, Special Issue 10: 49-60.

Martin, L.-P. 1980. Histoire de la chasse au Québec. Boréal Express. Montréal, Québec. 273 pages.

Messier, F. 1994. Ungulate population models with predation: a case study with North American moose. Ecology 75: 478-488.

Messier, F. 1995. Trophic interactions in two northern wolf-ungulate systems. Wildlife Research 22: 131-146.

Messier, F., J. Huot, J., D. Le Hénaff, and **S. Luttich.** 1988. Demography of the George River caribou herd: evidence of population regulation by forage and range expansion. Arctic 47: 279-287.

Moisan, G. 1956. Le caribou de Gaspé I. Histoire et distribution. Naturaliste canadien 83 (10): 225-234.

Moisan, G. 1957. Le caribou de Gaspé III. Analyse de la population et plan d'aménagement. Naturaliste canadien 84 (1): 5-27.

Morneau, C., and **S. Payette.** 1998. A dendroecological method to evaluate past caribou (*Rangifer tarandus L.*) activity. Écoscience 5: 64-76.

Ouellet, J.-P, J. Ferron, and **L. Sirois.** 1996. Space and habitat use by the threatened Gaspé caribou in southeastern Québec. Canadian Journal of Zoology 74: 1922-1933.

Paré, M. 1987. Effets du remplissage d'un réservoir hydro-électrique sur la population de caribous de Caniapiscau. M.Sc. thesis, Université Laval. Ste-Foy, Québec. 141 pages.

Payette, S., C. Morneau, L. Sirois, and **M. Despont.** 1989. Recent fire history of the northern Québec biomes. Ecology 70: 656-673.

Richard, P. J. H. 1993. Origine et dynamique postglaciaire de la forêt mixte au Québec. Review of Palaeobotany and Palynology 79: 31-68.

Schaefer J. A., A. M. Veich, F. H. Harrington, W. K. Brown, J. B. Theberge, and **S. N. Luttich.** 1999. Demography of decline of the Red Wine Mountains caribou herd. Journal of Wildlife Management 63: 580-587.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology 70: 1494-1503.

Seip, D. R., and **D. B. Cichowski.** 1996. Population ecology of caribou in British Columbia. Rangifer, Special Issue 9: 73-80.

Seton, E. T. 1953. Lives of game animals. Volume 3, part 1. G. T. Barnford Co., Boston, Massachusetts.

St. Cyr, D. N. 1873. Le renne du nord. Naturaliste canadien 5 (1): 16-32.

Vandal, D. 1985. Écologie comportementale du caribou du parc des Grands-Jardins. M.Sc. thesis, Université Laval. Ste-Foy, Québec. 128 pages.

Received 5 October 2001
Accepted 4 March 2004

The Wood Turtle, *Glyptemys insculpta*, at River Denys: A Second Population for Cape Breton Island, Nova Scotia.

ANDREAS GRÄF[1], JOHN GILHEN[2] and JILL D. ADAMS[3]

[1] Zollstockweg 1e, 64823 Gross-Umstadt, Germany
[2] Nova Scotia Museum of Natural History, 1747 Summer Street, Halifax, Nova Scotia B3H 3A6 Canada
[3] Cape Breton Highlands National Park, Ingonish Beach, Nova Scotia B0C 1L0 Canada

Gräf, Andreas, John Gilhen, and Jill D. Adams. 2003. The Wood Turtle, *Glyptemys insculpta*, at River Denys: A second population for Cape Breton Island, Nova Scotia. Canadian Field-Naturalist. 117(3): 415-418.

The Wood Turtle, *Glyptemys insculpta*, population at River Denys, Inverness County, Cape Breton Island, Nova Scotia, was unknown except locally until listed in a provincial survey in 1995. Subsequently a hatchling was photographed at McLennan Brook on 17 September 1999, and three adult males were photographed between 14 and 19 September 2000. Two adult females were photographed at South Side River Denys on 18 June 2001. An excavated nest and empty egg shells were located at the same time on a stony-gravel bank at the outflow of McLennan Brook, and one sub-adult male was found at the edge of a hay field on 19 August 2001. Additional observations made of a nesting site and five basking sites, mostly along the main branch of River Denys, provide further evidence that a breeding population of Wood Turtles exists in River Denys watershed.

Key Words: Wood Turtle, *Glyptemys insculpta*, River Denys, Inverness County, Bras D'or Lake Drainage, second breeding population, Cape Breton Island, Nova Scotia.

The Wood Turtle, *Glyptemys insculpta*, is easily distinguished from the Snapping Turtle, *Chelydra serpentina serpentina*, Blanding's Turtle, *Emydoidea blandingii*, and Eastern Painted Turtle, *Chrysemys picta picta*, which are also native to Nova Scotia, by its distinctive carapace shape and colour. The raised pyramid-like scutes, prominent central keel, and slight upward flare of the pointed posterior marginals give the Wood Turtle its unique shape. Its sculptured appearance earned it the specific name *insculpta*. The carapace is brown with black and yellow radiating streaks. The undersides of the neck and legs are typically orange but some individuals are red-orange. The Wood Turtle belongs to the largest family of turtles which includes the semiaquatic, pond and marsh turtles (Emydidae) [Conant and Conant 1991]. It is related to the Spotted (*Clemmys*), Western Pond (*Actinemys*) and Bog Turtle (*Glyptemys*) (Holman and Fritz 2001). Of these, only the Wood Turtle is native to the Canadian Maritimes where it is found in both Nova Scotia and New Brunswick. In Canada, it also occurs in southern Quebec and Ontario (Cook 1984); in the United States its distribution extends south to the Virginias and west to eastern Minnesota (Ernst et al. 1994).

The Wood Turtle probably colonized Cape Breton Island in early post-Wisconsin glaciation times, about 10000 YBP (years before present), before submergence of the land bridge which connected Cape Breton Island to mainland Nova Scotia (Bleakney 1958; Bousfield and Thomas 1975; Gilhen 1984. However, it was not recorded by Bleakney (1958) or Powell (1965) on Cape Breton Island. A breeding population was discovered in 1973 at River Inhabitants, Richmond County, 45°40'N, 61°14'W [=Cleveland] Atlantic Ocean Drainage (Gilhen and Grantmyre 1973). Here we report an additional breeding population at River Denys, Inverness County, 45°50'N, 61°10'W, Bras D'or Lake Drainage, the second population for Cape Breton Island (Figure 1).

River Denys occupies Theme Region 560 [Submerged Lowlands] (Davis and Browne 1997). In the north, headwaters streams drain Blues Mountain and the northern section of The Big Ridge, Theme Region 313a [Creignish Hills]. In the south, headwater streams drain North Mountain and MacIntosh Mountain, Theme Region 313b [North Mountain]. The origins of northern tributaries of River Inhabitants run very close to, and in some cases interdigitate, southern tributaries of River Denys. For example, a branch of McLennan Brook, River Denys watershed, is about 1 km west of MacCalls Brook, River Inhabitants watershed, and Wood Turtles likely travel from one watershed to the other. In recent years, the Trans Canada Highway (Route 105) to the north and Canadian National Railway to the south pass through both watersheds. Wood Turtles are very active along these man-created rights-of-way, because they provide foraging and nesting sites.

Cape Breton Island is the least studied area in Nova Scotia for amphibian and reptile faunas. The Wood Turtle population at River Denys, Inverness County, was unknown to science until Adams (1995) listed 33 localities from Ohio River area, Shelburne County, to North Aspy River, Victoria County as a result of public surveys she conducted. Evidence that a breeding population of Wood Turtle actually existed at River Denys, however, was not discovered until 17 September 1999, at 1535 hours. A. G. photographed one hatchling beside the bridge at highway west of River Denys Centre. On 14 September 2000, at 1005 hours, he photographed an

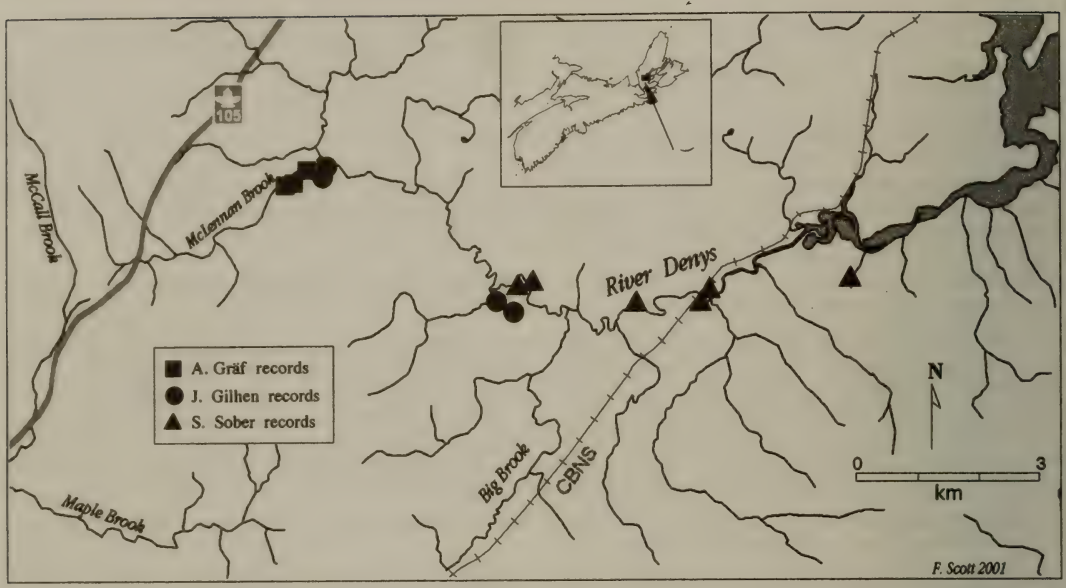


FIGURE 1. Localities where Wood Turtles, *Glyptemys insculpta*, have been observed at River Denys, Inverness County, Cape Breton Island, Nova Scotia. Squares are localities recorded by Andreas Gräf; circles by John Gilhen; and triangles by Stephen W. Sober.

adult male basking in the sun on the shore of McLennan Brook adjacent to a hay field, immediately downstream from the bridge at South Side River Denys Road (Figure 2). On 19 September 2000, at 1115 hours, a second adult male was found basking in the sun on the stony gravel shore, between overhanging sedges, just upstream from the bridge. At 1205 hours, just 10 m upstream from the second adult male, a third adult male was found basking in the sun on the shore.

J. G. photographed two adult females on a road bank at South Side River Denys Road on 18 June 2001. One female was observed digging a nest near a dry stream bed at 0830 hours. She deposited six eggs and had completely covered them by 1000 hours (Cover). The second individual, a spent female, was found near Morleys Brook at 1030 hours. On 19 August 2001, at 1055 hours, a disfigured, probably by farm machinery, sub-adult male (Figure 3) was observed eating dandelion greens at the edge of a hay field adjacent to River Denys. This remarkably healed individual passed nine Choke-cherry pits while being photographed. At 1220 hours, a excavated nest by a predator and empty egg shells was discovered on the crown of a stony-gravel bank at the outflow of McLennan Brook into River Denys.

FIGURE 2. Adult male Wood Turtle, *Glyptemys insculpta*, observed at McLennan Brook, River Denys Watershed, Inverness County, Cape Breton Island, Nova Scotia, on 14 September 2000 by Andreas Gräf.

Stephen M. Sober, a resident of River Denys area, provided us with localities for one Wood Turtle nesting site and five basking sites, which he observed while canoeing mostly along the main branch of River Denys. Our observations along with Stephen M. Sober's confirm a breeding population of Wood Turtles exists at River Denys Watershed. Copies of all colour transparencies as well as colour and black-and-white photographs have been deposited in the Nova Scotia Museum of Natural History.

Glyptemys insculpta is a stream turtle in Nova Scotia. Although individuals may be found throughout certain watersheds, the main population is centered in slow moving meandering sections through fertile valleys. Here, along extensive intervals, meadows and oxbow ponds, streams are typically banked mostly by alders and widely-spaced dead Elm Trees. At River Denys,

FIGURE 3. Disfigured sub-adult male Wood Turtle, *Glyptemys insculpta*, discovered at edge of a hayfield near McLennan Brook, River Denys Watershed, Inverness County, Cape Breton Island, Nova Scotia, on 19 August 2001 by John Gilhen.

Speckled Alder, *Alnus incana*, and Choke-cherry, *Prunus virginiana*, are the dominant trees along the river bank. Also at River Denys extensive meadows have been developed into hay fields. The meandering river has deep sections where the Wood Turtles hibernate. Stony-gravel and sandy-gravel deposits usually on bends in the river are natural nesting sites. Nurseries for hatchlings have not been described in Nova Scotia and juveniles are rarely observed. Wet meadows provide excellent foraging habitat. Meadows which have been developed into hay fields usually have residual meadow and old field vegetation along the edge which Wood Turtles frequent to feed on vegetation, berries and invertebrates.

Unlike the Blandings Turtle, which is protected within Kejimkujik National Park, there is not one Nova Scotia Wood Turtle population or critical habitat which is completely protected in a national or provincial park. (Gilhen et al. 1994). The Wood Turtle under the "General Status Ranks of Wildlife in Nova Scotia" by Nova Scotia Department of Natural Resources is listed as "Yellow, sensitive to human activities or natural events".

Wood Turtle populations in Nova Scotia are thought to have been declining for a number of years due mainly to the removal of adults from their native stream by campers and fishermen. As well, females crossing roads to nesting sites are either killed or intercepted by the traveling public, who desire to keep them for pets (Gilhen et al. 1994). Most of these collected turtles either escape captivity or are released, sometimes far removed from their native stream. In the United States, from 1970 to 1974 Carroll and Ehrenfeld (1978) documented 189 sub-adult and adult Wood Turtles moved from 52 home sites near Accord, New York, to a common release point. Displacement ranged from 0.35 to 50 km. The turtles were subsequently tagged and released. Homing was frequent back to the exact site of first capture but success fell off sharply when displacement distance exceeded 2.0 km. The Nova Scotia Museum of Natural History, Halifax, and Turtle Watch, along with the Herp Atlas, Acadia University, Wolfville, continue to receive verbal reports of Wood Turtles from all regions of Nova Scotia. We believe many of these are escaped or released captives (Gilhen et al. 1994).

As the opening of areas of wilderness in Nova Scotia for recreational purposes continues Wood Turtle populations are increasingly exposed to human interference and habitat degradation. The potential effects of this are indicated by a 20-year (1974 to 1993) study of the effects of human recreation on two Wood Turtle populations in Connecticut, USA (Garber and Burger 1993). During the first nine years (1974 to 1982) of the study people were denied access to the property and Wood Turtle populations remained stable. During the second nine years (1983 to 1991) when the property was opened to human recreation both Wood Turtle populations declined steadily, 87% in nine years and by almost 100% in 10 years.

Acknowledgments

The authors are grateful to Stephen M. Sober for providing us with his Wood Turtle observations at River Denys. Fred Scott made the distribution map of River Denys. Roger Lloyd, Learning Resources and Technology, Nova Scotia Department of Education, selected the best colour negative and colour transparencies and developed these to provide us with the black and white photographs required for figures 2, and 3 and cover. Andrew Hebda, Curator of Zoology, Nova Scotia Museum of Natural History, and two anonymous reviewers made useful comments on the manuscript.

Literature Cited

Adams, J. D. 1995. An evaluation of wood turtle (*Clemmys insculpta* LeConte) distribution in Nova Scotia through public surveys. Honours B. Sc. thesis, Acadia University, Wolfville, Nova Scotia. 48 pages.

Bleakney, J. S. 1958. A zoogeographical study of the amphibians and reptiles of eastern Canada. National Museum Canada, Bulletin 155. 199 pages.

Bousfield, E. L., and **M. L. H. Thomas.** 1975. Postglacial change in distribution of littoral marine invertebrates in the Canadian Atlantic region. Proceedings of the Nova Scotian Institute of Science, Supplement 3: 47–60.

Carroll, T. E., and **D. W. Ehrenfeld.** 1978. Intermediate-range homing in the Wood Turtle, *Glyptemys insculpta.* Copeia 1978: 117–126

Conant, R., and **J. T. Collins.** 1991. A field guide to reptiles and amphibians of eastern and central North America – Third edition, Houghton Mifflin Company, Boston.

Cook, F. R. 1984. Introduction to the amphibians and reptiles of Canada. National Museum of Natural Sciences, National Museums of Canada. 211 pages.

Davis, D. S., and **S. Browne.** 1997. Natural History of Nova Scotia. Volume 2, Theme Regions, Nova Scotia Museum, Halifax. 304 pages.

Ernst, C. H., R. W. Barbour, and **J. E. Lovich.** 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington. 578 pages.

Garber, S. D., and **J. Burger.** 1993. Effects of human recreation on the North American Wood Turtle (*Clemmys insculpta*): A 20 year study (1974–1993). Conservation, restoration, and management of tortoises and turtles – an international conference, July 11–16, 1993. State University of New York. Purchase, New York U.S.A.

Gilhen, J. 1984. Amphibians and reptiles of Nova Scotia. Nova Scotia Museum, Halifax. 162 pages.

Gilhen, J., and **B. Grantmyre.** 1973. The Wood Turtle, *Clemmys insculpta* (LeConte): An addition to the herpetofauna of Cape Breton Island, Nova Scotia. Canadian Field-Naturalist 87: 308–310.

Gilhen, J., T. Herman, and **N. Meister.** 1994. Wood Turtles face uncertain future. Conservation 18: 5–7.

Holman, J. A., and **U. Fritz**. 2001. A new emydine species from the Middle Miocene (Barstovian) of Nebraska, USA with a new generic arrangement for the species of *Clemmys* sensu McDowell (1964) (Reptilia: Testudines: Emydidae). Zoologische Abhandlungen, Staatliches Museum für Tierkunde Dresden 51 (20): 331-353.

Powell, C. B. 1965. Zoogeography and related problems of turtles in Nova Scotia. B.Sc. thesis, Acadia University, Wolfville, Nova Scotia. 84 pages.

Received 27 October 2001
Accepted 14 January 2004

Limits to Plasticity in Gray Wolf, *Canis lupus*, Pack Structure: Conservation Implications for Recovering Populations

THOMAS M. GEHRING[1], BRUCE E. KOHN[2], JOELLE L. GEHRING[1], and ERIC M. ANDERSON[3]

[1] Department of Biology, Central Michigan University, Mt. Pleasant, Wisconsin 48859 USA
[2] Wisconsin Department of Natural Resources, Ranger Station, Box 576, Rhinelander, Wisconsin 54501 USA
[3] College of Natural Resources, University of Wisconsin-Stevens Point, Stevens Point, Wisconsin 54481 USA

Gehring, Thomas M., Bruce E. Kohn, Joelle L. Gehring, and Eric M. Anderson. 2003. Limits to plasticity in Gray Wolf, *Canis lupus*, pack structure: conservation implications for recovering populations. Canadian Field-Naturalist 117(2): 419–423.

We documented the dynamics of the Five Corners Pack (FCP) in east-central Minnesota and northwestern Wisconsin through the loss and replacement of four alpha-females over a four-year period. This pack remained intact and produced offspring during the period despite the annual loss of the alpha female. However, we observed a disintegration of the pack after four consecutive alpha females died, at least two of which were due to illegal killing by humans. Our observations generally support the hypothesis that "single-parent" wolf packs may be more prevalent in areas with low densities of wolves and high densities of ungulate prey. Our observations also highlight the need to assess the potential negative impacts of wolf removal on pack structure and persistence at local and regional scales.

Key Words: Gray Wolf, *Canis lupus*, disease, edge effects, behavior, mortality, radio telemetry, recovering populations, social structure, Minnesota, Wisconsin.

During 1992-1996, we monitored Gray Wolves (*Canis lupus*) by means of radio telemetry as part of a larger study on the effects of highway development on wolf movements and population dynamics (Gehring 1995; Kohn et al. 1995*, 1999*, 2000*). Herein, we report on the plastic nature of pack structure and reproductive ecology of the Five Corners Pack (FCP) in east-central Minnesota and northwestern Wisconsin. We also highlight the limits to this plasticity relative to the disintegration of pack dynamics coincident with dispersal and high rates of mortality for reproducing females. Although limited to intensive observations of one pack, our results have implications for the management of wolf populations in the upper Midwest.

Methods

Wolves were captured in east-central Minnesota and northwestern Wisconsin during May-August in modified #14 Newhouse steel traps (Kuehn et al. 1986). Captured wolves were immobilized by an intra-muscular injection of ketamine hydrochloride and xylazine hydrochloride. Once immobilized, wolves were fitted with a radio collar and ear-tagged with a uniquely numbered plastic tag (Kohn et al. 2000*). Radio-collared wolves were monitored by radio telemetry at least 1-2 times weekly from fixed-wing aircraft (Mech 1974), and an attempt was made to relocate individuals daily using a vehicle-mounted antenna system (Gehring 1995; Shelley and Anderson 1995*). We maintained a minimum of one radio-collared wolf in each study pack.

Radio telemetry was used to determine movements, home range, and population dynamics of wolves in our study area. Additionally, we conducted howling surveys during July-September each year to assess pup production (Harrington and Mech 1982; Fuller and Sampson 1988). We also used howling surveys and track counts in the fall and winter to determine recruitment of pups into wolf packs and pack size (Rothman and Mech 1979; Harrington and Mech 1982; Kohn et al. 2000*).

Results

Temporal Dynamics

The FCP consisted of one to seven wolves during the study period; however, pack composition (most notably alpha-females) differed between years (Gehring 1995). During fall 1991, W149 (alpha-female 1) dispersed from the Moose Lake Pack in northwestern Wisconsin (approximately 70 km northeast of the FCP) to the FCP and assumed alpha status, joining four other wolves. Thus, alpha-female 1 likely replaced the previous FCP alpha-female. During May 1992, the Wisconsin Department of Natural Resources captured and radio-collared a yearling female wolf (W177, Wydeven 1994*). Based on howling surveys, we determined that alpha-female 1 produced an estimated six pups before her death in June 1992. Alpha-female 1's carcass was found discarded along a roadside near the northern extent of the FCP territory (Shelley and Anderson 1995*; Gehring 1995). Necropsy results indicated that she had been killed in a snare (Kohn et al. 1995*, 2000*). After the death of alpha-female 1, W177 (yearling female) dispersed from the FCP and eventually formed the Price Creek Pack in north-central Wisconsin (Wydeven 1994*). Based on howling surveys and track counts, we determined that a minimum of two pups survived into the winter (Gehring 1995).

In August 1992, W145 (alpha-female 2) dispersed to the FCP from the Crotte Creek Pack in northwestern

Wisconsin (approximately 50 km northeast of the FCP). Based on the arrival date of alpha-female 2 into the FCP, we determined that she likely aided in the rearing of alpha-female 1's pups. Our howling surveys indicated that alpha-female 2 successfully produced an estimated four pups in 1993 before her death in late July 1993 by apparently illegal means. Our howling surveys later confirmed that all pups survived into the fall. Although her carcass was never recovered, alpha-female 2's cut-off collar was found in a stream near Minnesota State Highway 48 (approximately 3.5 km east of the site where the carcass of alpha-female 1 was found). In 1993, the FCP contained an estimated three adult/yearling wolves (including W188, a radio-collared yearling male) after the death of alpha-female 2. However, based on howling surveys and track counts, we estimated that the pack had grown to seven members by winter 1994 (Gehring 1995).

Concurrent with events in the FCP, during winter 1992-93 and 1993-94, two wolf packs bordering the FCP maintained three wolves (Crex Meadows Pack, south of FCP) and up to five wolves (Sand Creek Pack, northwest of FCP, Figure 1). During summer 1993, the United States Department of Agriculture Animal and Plant Health Inspection Service, Wildlife Services (APHIS-WS), killed five wolves in the Sand Creek Pack (SCP) following livestock depredations, and this was believed to be the end of this pack (Wydeven and Megown 1996a*). During spring 1994, W188 (male from FCP) dispersed to the former SCP territory and re-established the pack with one other wolf.

During May 1994, we captured an lactating adult female wolf (W221) in the FCP. This wolf, which became W221 (alpha-female 3), originally had been captured and ear-tagged as a pup in the Rainbow Lake Pack, northwestern Wisconsin (approximately 120 km northeast of the FCP). Based on her arrival date into the FCP, alpha-female 3 likely aided in the rearing of alpha-female 2's pups. Alpha-female 3 produced a minimum of one pup during 1994 (Gehring 1995). During winter 1994-1995, the FCP was believed to contain only two wolves, whereas the Crex Meadows Pack (CMP) had grown to eight wolves and the CMP began using the southern portion of the FCP territory (Wydeven and Megown 1996a*). During winter 1995-1996, the FCP contained W221 and a possible second wolf (Wydeven and Megown 1996b*). In May 1996, alpha-female 3 was killed by intra- or inter-pack strife north of the previous boundary of the FCP territory (Kohn et al. 2000*, Figure 1). During June-July 1996, APHIS-WS also killed four wolves in the SCP as part of depredation-control activities. Following the death of alpha-female 3, the FCP structure appears to have disintegrated and the adjacent CMP remained in the southern half of the former FCP territory (Kohn et al. 1995*, 1999*; Wydeven and Megown 1996a). During 1996-1998, no additional signs of the FCP were reported, whereas the CMP maintained an estimated three wolves (Wydeven and Cervantes 1997*; Wydeven et al. 1998*).

Discussion

Boyd and Jimenez (1994) reported three cases of lone wolves and two instances where a pack of female wolves successfully reared young after the death of a mate. Boyd and Jimenez (1994) suggested that the successful rearing of pups by packs that contain only one surviving mate may have been related to the low density of wolves and high density of ungulate prey in their study area. Data from the FCP may lend some support to this hypothesis. Wolf densities in our study area were low (2-3 wolves/1000 km^2; Gehring 1995), and deer densities in the FCP were high (8.5-8.9 deer/km^2; Gehring 1995). However, we suggest that the FCP was unique because it successfully reared pups ranging in ages from 8-13 weeks old over three consecutive years despite the annual loss of the alpha-female. The short-term maintenance of the FCP was aided by the high fecundity of these females and the rapid replacement of alpha-females each year. However, the instability in the FCP structure, due to natural mortality and consistently high human-caused mortality, probably led to the ultimate demise of this pack, highlighting the ephemeral nature of wolf packs in a recovering wolf population, particularly in semi-agricultural landscapes.

Managing Wolf Populations

Our observations also highlight the need to incorporate the complexity of wolf pack dynamics into long-term wolf management plans and policies in the Great Lakes Region as well as other regions. In particular, wolf removal as part of livestock-depredation programs can alter wolf pack composition (Gehring 1995). Policy makers developing wolf depredation management strategies should therefore assess the potential negative impacts of wolf removal on pack structure and persistence, especially in recovering populations (Haber 1996). The proposed zone system for wolf management, whereby different areas have different management prescriptions, in the Great Lakes Region (Mech 1995; Wisconsin Department of Natural Resources 1999*; Minnesota Department of Natural Resources 2001*) may lead to locally unstable pack dynamics if sink habitats are formed by depredation control or harvest activities. Under a zone system, an established wolf pack near the edge of a protected zone may still be vulnerable to external human-related mortality (Woodroffe and Ginsberg 1998; Laurance 2000). Furthermore, all wolves dispersing from established wolf packs in the protected zone could be vulnerable. Woodroffe and Ginsberg (1998) demonstrated vulnerability to populations of large mammalian carnivores due to edge effects in the form of human-caused mortality outside of reserves (i.e., edge effects expressed over large spatial scales, *sensu* Laurance 2000). Carnivores with large home ranges were most

FIGURE 1. Location of wolf packs monitored during 1992-96 in Pine County, Minnesota and Burnett County, Wisconsin. Abbreviations include: CMP = Crex Meadows Pack; FCP = Five Corners Pack; SCP = Sand Creek Pack. The star indicates the location where W221 was found dead in 1996.

vulnerable independent of local population densities, suggesting that the formation of population sinks at reserve margins leads to depleted carnivore numbers and might ultimately lead to the extinction of the reserve population (Woodroffe and Ginsberg 1998).

We draw a parallel to the present discussion in the Great Lakes Region relative to various proposals to establish a management zone system across both Minnesota and Wisconsin for wolf management (Wisconsin Department of Natural Resources 1999*; Minnesota Department of Natural Resources 2001*). Zones would differ relative to the extent to which lethal control and translocation are allowed. For example, northern regions of Wisconsin would serve as a quasi-reserve (i.e., some lethal control and translocation is allowed) for wolves, whereas southern Wisconsin would be a wolf-free zone with potentially high rates of mortality (e.g., mortality due to vehicular collisions and active killing by humans) for wolves occupying this zone (Wisconsin Department of Natural Resources 1999*). We suggest that such a management scenario could result in edge effects on zones where wolves are afforded more protection by the formation of sink habitats in adjacent management zones, thereby jeopardizing the viability of wolves in more protected zones.

Our observations on the FCP suggest that this pack's region may have served as a sink habitat for a large portion of Wisconsin's recovering wolf population. Thus, the presence of sink habitats, particularly on the periphery of recovering populations, could potentially slow the recovery process. We base this suggestion on the temporarily high replacement rate of alpha females in the FCP, all of which dispersed out of the recovering Wisconsin population. We suggest that wolf management plans in the Great Lakes Region must incorporate scientifically-based strategies for ameliorating the potential negative impacts of large-scale edge effects on wolf pack structure and long-term population viability.

Conservation Implications

One strategy, in addition to public education, that might (1) reduce the mortality of wolves associated with depredation control activities; (2) reduce wolf-human conflicts (e.g., illegal killing); and (3) minimize the instability of pack dynamics, would be an *in situ* management approach of depredation. That is, rather than using a reactionary approach by removing wolves on a case-by-case basis, managers might use proactive management by taking an integrated approach (*sensu* Fritts et al. 1992*) and attempt to reduce or prevent depredations caused by resident wolves (Gehring et al. 1996). Such an approach could include the use of non-lethal tools as part of an arsenal of preventative measures for reducing depredations. These measures might include: improved livestock husbandry (Gehring et al. 1999), the use of shock-collars (Hawley et al. 2003), and the use of guard animals.

Acknowledgments

Funding and logistical support were provided by the Wisconsin Department of Natural Resources (Federal Aid in Wildlife Restoration Act, Pittman-Robertson Project W-141-R); Wisconsin Department of Transportation; and University of Wisconsin-Stevens Point. We also thank the Minnesota Department of Natural Resources, USDA APHIS-Wildlife Services, and U. S. Fish & Wildlife Service for additional logistical support of this study. We thank J. B. Dunning, Jr. for his constructive comments that improved the manuscript.

Documents Cited (marked * in the text)

Fritts, S. H., W. J. Paul, L. D. Mech, and **D. P. Scott.** 1992. Trends and management of wolf-livestock conflicts in Minnesota. United States Fish and Wildlife Service Resource Publication Number 181.

Kohn, B. E., D. P. Shelley, T. M. Gehring, D. M. Unger, and **E. M. Anderson**. 1995. Impacts of Highway 53 development on timber wolves. Wisconsin Department of Natural Resources. Report #3. 17 pages.

Kohn, B., J. Frair, D. Unger, T. Gehring, D. Shelley, E. Anderson, and **P. Keenlance.** 1999. Impacts of a highway expansion project on wolves in northwestern Wisconsin: preliminary findings. Proceedings of The International Conference on Wildlife Ecology and Transportation III, Missoula, Montana.

Kohn, B., J. Frair, D. Unger, T. Gehring, D. Shelley, E. Anderson, and **P. Keenlance**. 2000. Impacts of the U.S. Highway 53 expansion project on wolves in northwestern Wisconsin: final report. Wisconsin Department of Natural Resources. 49 pages.

Minnesota Department of Natural Resources. 2001. Minnesota wolf management plan. St. Paul, Minnesota. 80 pages.

Shelley, D. P., and **E. M. Anderson**. 1995. Effects of vehicular traffic on and ecology of timber wolves in northwestern Wisconsin and east-central Minnesota. Final Report. University of Wisconsin-Stevens Point, Stevens Point. 100 pages.

Wisconsin Department of Natural Resources. 1999. Wisconsin wolf management plan. Madison, Wisconsin. PUBL-ER-099 99. 74 pages.

Wydeven, A. P. 1994. Status of the timber wolf in Wisconsin. Wisconsin Endangered Resources Report #102. Wisconsin Department of Natural Resources. 20 pages.

Wydeven, A. P., and **N. M. Cervantes**. 1997. Progress report of wolf population monitoring in Wisconsin for the period April – September 1997. Wisconsin Department of Natural Resources. 20 pages.

Wydeven, A. P., and **R. A. Megown**. 1996a. Progress report of wolf population monitoring in Wisconsin for the period October – December 1995. Wisconsin Department of Natural Resources. 11 pages.

Wydeven, A. P., and **R. A. Megown**. 1996b. Progress report of wolf population monitoring in Wisconsin for the period April – June 1996. Wisconsin Department of Natural Resources. 18 pages.

Wydeven, A. P., B. E. Kohn, R. P. Thiel, R. N. Schultz, and **S. R. Boles**. 1998. Progress report of wolf population monitoring in Wisconsin for the period April – September 1998. Wisconsin Department of Natural Resources. 16 pages.

Literature Cited

Boyd, D. K., and **M. D. Jimenez**. 1994. Successful rearing of young by wild wolves without mates. Journal of Mammalogy 75: 14-17.

Fuller, T. K., and **B. A. Sampson**. 1988. Evaluation of a simulated howling survey for wolves. Journal of Wildlife Management 52: 60-63.

Gehring, T. M. 1995. Winter wolf movements in northwestern Wisconsin and east-central Minnesota: a quantitative approach. M.S. thesis, University of Wisconsin-Stevens Point, Stevens Point. 132 pages.

Gehring, T. M., J. L. Gehring, and **B. E. Kohn**. 1999. Management of wolf-caused livestock depredations: the farmer's role. 129th Annual Conference of the Wisconsin Academy of Sciences, Arts and Letters. Stevens Point, Wisconsin.

Gehring, T. M., J. L. Gehring, M. A. Beckel, and **M. A. Callahan.** 1996. Recovering wolf populations. Conservation Biology 10: 5-6.

Haber, G. C. 1996. Biological, conservation, and ethical implications of exploiting and controlling wolves. Conservation Biology 10: 1068-1081.

Harrington, F. H., and **L. D. Mech.** 1982. An analysis of howling response parameters useful for wolf pack censusing. Journal of Wildlife Management 46: 686-693.

Hawley, J. E., T. M. Gehring, S. Rossler, R. N. Schultz, and **A. P. Wydeven**. 2003. Experimental assessment of a non-lethal control method for reducing conflict. World Wolf Congress, Banff, Alberta, Canada.

Kuehn, D. W., T. K. Fuller, L. D. Mech, W. J. Paul, S. H. Fritts, and **W. E. Berg**. 1986. Trap-related injuries to gray wolves in Minnesota. Journal of Wildlife Management 50: 90-91.

Laurance, W. F. 2000. Do edge effects occur over large spatial scales? Trends in Ecology and Evolution 15: 134-135.

Mech, L. D. 1974. Current techniques in the study of elusive wilderness carnivores. Pages 315-324 *in* Proceedings of the eleventh international congress on game biology, Stockholm, Sweden.

Mech, L. D. 1995. The challenge and opportunity of recovering wolf populations. Conservation Biology 9: 270-278.

Rothman, R. J., and **L. D. Mech.** 1979. Scent marking in lone wolves and newly formed pairs. Animal Behavior 17: 750-760.

Woodroffe, R., and **J. R. Ginsberg.** 1998. Edge effects and the extinction of populations inside protected areas. Science 280: 2126-2128.

Received 5 November 2001
Accepted 19 January 2004

Den Site Activity Patterns of Adult Male and Female Swift Foxes, *Vulpes velox*, in Northwestern Texas

PATRICK R. LEMONS[1,2], WARREN B. BALLARD[1], ROBERT M. SULLIVAN[3], and MARSHA A. SOVADA[4]

[1] Department of Range, Wildlife and Fisheries Management, Texas Tech University, Box 42125, Lubbock, Texas 79409 USA
[2] Current Address: Department of Natural Resource and Environmental Sciences, University of Nevada-Reno, 1000 Valley Road, Reno, Nevada 89512 USA
[3] Texas Parks and Wildlife Department, P. O. Box 659, Canyon, Texas 79015 USA
[4] U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 37th Street Southeast, Jamestown, North Dakota 58401 USA

Lemons, Patrick R., Warren B. Ballard, Robert M. Sullivan, and Marsha A. Sovada. 2003. Den site activity patterns of adult male and female Swift Foxes, *Vulpes velox*, in northwestern Texas. Canadian Field-Naturalist 117(3): 424-429.

Activity of Swift Foxes (*Vulpes velox*) at den sites was studied in northwestern Texas during pup rearing seasons in 2000 and 2001 to determine role of males in parental care. Twenty-four percent of radio-collared females with a potential to breed successfully raised pups to eight weeks of age. We intensively monitored presence and absence of male and female Swift Foxes at two den sites each year. Females were present >2.6 times more at den sites than males during the pup rearing season. Female and male Swift Foxes largely stayed at dens during diurnal hours and were active away from dens during nocturnal and crepuscular hours. Females and males spent 12.4% and 3.0% more time at dens before pups emerged, than after pups emerged, respectively. Following depredation of one male parent, the female spent 29% less time at the den site. Decrease in time spent at the den by the female following loss of her mate suggested that loss of one parent might severely impact recruitment of Swift Foxes. Our observations indicated that intense Coyote (*Canis latrans*) depredation may severely impact pup-rearing success as well as the parental care within Swift Fox family groups.

Key Words: Swift fox, *Vulpes velox*, den sites, helping behavior, Texas.

Understanding the importance of parental behavior in rearing offspring is an important management consideration. Parental investment theory suggests that efforts parents dedicate to caring for young are at the expense of later reproduction (e.g., decreased fecundity in subsequent years or decreased survival) (Williams 1966; Trivers 1972). Increased parental investment can decrease survival of adults through increased susceptibility to depredation or decreased physiological fitness (Krebs and Davies 1998). This phenomenon has been documented in numerous species (Gustafsson and Sutherland 1988; Sterns 1992). For example, in Great Tits (*Parus major*), increased brood sizes increase susceptibility of parents to infection from malaria and haematozoans (Norris et al. 1994; Richner et al. 1995). Winter mortality in Kestrels (*Falco tinnunculus*) increased as parental effort in the previous summer increased (Daan et al. 1996). Knowing parental investment of species is important to understanding the impacts of changes in social structures on reproductive success.

Swift Fox reproductive behavior has not been thoroughly studied. Available literature suggests that Swift Foxes are primarily monogamous breeders, and both parents share in pup rearing (Kilgore 1969; Egoscue 1979; Scott-Brown et al. 1987; Samuel and Nelson 1992). However, roles of male and female Swift Foxes in parental care have not been identified. The role each parent has in pup rearing could be an important factor in successful raising of pups as well as the impacts on future health of parents following pup rearing.

Additional females known as "helpers" have been documented at natal dens of Swift Foxes (Egoscue 1979; Scott-Brown et al. 1987; Covell 1992; Samuel and Nelson 1992; Kitchen et al. 1999). Red Foxes (*Vulpes vulpes*), Arctic Foxes (*Alopex lagopus*), and Kit Foxes (*Vulpes macrotis*) have also been documented with helpers at natal dens (Macdonald 1983; Macdonald and Moehlman 1983; Moehlman 1989; Spiegel and Tom 1996). Helpers have been documented to increase overall pup rearing success in family groups of Red Foxes, Arctic Foxes, and Blackbacked Jackals (*Canis mesomelas*) (Macdonald 1979, 1983; Moehlman 1979, 1989; Macdonald and Moehlman 1983). However, no information exists concerning the role helpers have in Swift Fox family groups and their impacts on pup rearing success.

In Kit Foxes, helping behavior appears rare, which may be due to high mortality of individuals through intense Coyote depredation (Koopman et al. 2000; Kamler et al. 2003). In Swift Fox family groups in southeastern Colorado, 100% (n = 5) of helpers were found in Coyote reduction areas suggesting that increased Coyote depredation reduced occurrence of helpers (Covell 1992). It has been suggested that Swift Fox pup rearing success in family groups without helpers are more heavily impacted by intense Coyote depredation than in family groups with helpers (i.e., in

ocial groups with helpers, if an adult dies helpers can take over) (Covell 1992). Understanding the roles of helpers in Swift Fox family groups and their impacts on pup rearing success is important to determining if Coyotes indirectly decrease Swift Fox recruitment.

We studied pup-rearing behavior of adult male and female Swift Foxes in northwestern Texas to determine their roles in parental care. Parental behavior was studied to determine if differences existed between two different landscapes, as pups aged, and with the depredation of a male in one family group. Frequency of helpers in Swift Fox family groups as well as proportion of known females breeding were also recorded to determine impacts of intense Coyote depredation within the populations studied.

Study Area

Research was conducted at two 93 km^2 study sites in northwestern Texas. The first study site was designated our continuous rangeland landscape and was located 55 km west of Stratford in Dallam County, Texas, predominantly within the Rita Blanca National Grasslands. The area was restored short-grass prairie habitat dominated by Blue Grama (*Bouteloua gracilis*) and Buffalograss (*Buchloe dactyioides*) and was moderately to heavily grazed by cattle.

The Rita Blanca National Grasslands study site averaged 1250 m in elevation. Average temperature was 12.6°C with an average maximum daily temperature of 21.5°C and an average minimum daily temperature of 3.6°C. Average precipitation was 0.40 m per year with 0.31 m of snow per year (National Oceanic and Atmospheric Administration 2000, 2001).

The second study site was designated our fragmented agriculture/rangeland landscape and was located on a private ranch in Sherman County, Texas approximately 12 km south of Stratford, Texas. This site was composed of a mixture of short-grass prairie rangeland (35%), cultivated fields (31%), and conservation reserve program (CRP) (35%). Crops included corn, winter wheat, and sorghum. CRP land had either been recently enrolled in the program and was planted to warm-season grasses including Sideoats Grama (*Bouteloua curtipendula*), Blue Grama, Sand Dropseed (*Sporobolus cryptandrus*), and Buffalograss, or had not been recently reenrolled in the program and was vegetated by Old World Bluestem (*Bothriochloa* spp.).

The Sherman County study site averaged 1125 m in elevation. Average temperature was 13.4°C (average maximum daily temperature was 21.8°C, average minimum daily temperature was 5.0°C). Average precipitation was 0.44 m per year with 0.41 m of snow per year (National Oceanic and Atmospheric Administration 2000, 2001).

Methods

We located radio-collared Swift Foxes approximately twice per week from January through June of 2000 and 2001. We identified potential breeding pairs and pairs with helpers by monitoring foxes for shared den use. Radio-collars were equipped with mortality sensors allowing early detection of mortality and identification of causes of death. We identified dens used by radio-collared foxes and then monitored the dens where presence of pups was established.

Each year during the pup-rearing period (April through June), a den in each study site was monitored intensively with a den site activity station. Activity stations were placed 60 to 75 m from dens and consisted of a receiver, a Rustrak® recorder, and 12-volt battery placed in a weather-protected container, and a directional antenna placed on a mast 1.5 m above ground. Presence and absence of Swift Foxes at den sites were recorded once every 12 minutes on an 18.3 m tape advancing at 15.2 cm per hour. To calibrate the monitors, we placed a radio transmitter on a 0.2 m pole located 1 to 2 m behind the den. This transmitter was also recorded once every 12 minutes enabling our calibration of times on the tape to the actual time as marked on the tape with each daily visit.

To determine Swift Fox whelping dates, female foxes were systematically trapped until lactation was observed. Visual observations of dens were made at least twice per week to determine dates pups first emerged from dens, post emergent litter sizes, and number of pups successfully raised to eight weeks of age. We backdated four weeks from date pups were first observed to confirm whelping dates (Scott-Brown et al. 1987; Samuel and Nelson 1992). Observations were conducted with binoculars and spotting scopes from a distance of 75 to 100 m from the den between 3 hr before sunset to 30 minutes after sunset during the pup rearing period.

Presence and absence observations were combined across days and grouped by hour to determine activity of both male and female Swift Foxes. Differences in occurrence of male and female Swift Foxes at den sites were determined by comparing percentage of time spent at den sites. We also examined differences in time spent at den sites for pre- (first four weeks of monitoring) and post- (second four weeks of monitoring) emergent times as well as between landscapes. Sample variances (s^2) for percentage of time spent at den sites were determined (Zar 1999).

Results

Twenty-five female Swift Foxes were monitored in 2000 (n = 12) and 2001 (n = 13). Of these, 17 females' fates were determined to pup rearing season. Five showed signs of whelping, of which four successfully raised pups to eight weeks of age. Of the 12 remaining possible breeding females, five did not breed as a result of mortalities within the breeding pair, and seven were non-breeding single females. Two possible were documented prior to whelping, and both did not successfully whelp due to Coyote depredation within the Swift Fox family group.

TABLE 1. Duration of den site monitoring and den attendance of Swift Foxes in northwestern Texas during pup rearing season, 2000 and 2001.

	Den site monitoring			Presence (%)	
Den site	Date started	Date ended	Number of days monitored	Male	Female
PR-2000	9 April 2000	6 June 2000	58	38.0	66.2
RB-2000	6 April 2000	1 June 2000	56	21.5	61.7
PR-2001	9 April 2001	4 June 2001	56	9.1	54.0
RB-2001	15 April 2001	19 May 2001	30	70.5	28.9

Den site activity was monitored for 3360 hours for both male and female Swift Foxes. Overall, female Swift Foxes spent more time (63.1%, s^2 = 0.5%) at den sites than males (24.3%, s^2 = 1.5%). Percentage of time spent at den sites was variable between sexes (Table 1). At each den, differences between amount of time females and males spent at dens were also variable (2000 Rita Blanca den: 40.3%; 2000 Sherman County den: 28.2%; 2001 Rita Blanca den: 47.9%; 2001 Sherman County den: 44.9%).

Female Swift Foxes were away from dens during nocturnal hours, and were likely to be present at dens during diurnal hours (Figure 1). Females left dens around dusk and returned around dawn (Figure 1). Male Swift Foxes showed this same activity pattern; however, the pattern was not as distinct as that of female Swift Foxes (Figure 2). We did not observe any seasonal shift in adult movement patterns as the pups aged during this study.

Percentage of time spent at den sites changed for both males and females as Swift Fox pups aged. Males spent 25.5% (s^2 = 1.9%) of their time at dens prior to emergence and 22.4% (s^2 = 0.6%) of their time at dens following pup emergence. Females spent 68.0% (s^2 = 1.1%) of their time at den sites prior to emergence and 55.6% (s^2 = 3.7%) of their time at dens following pup emergence.

No difference in parental behavior was recorded for males or females when comparing the two landscapes. Males spent 24.0% (s^2 = 0.006%) of their time at den sites on continuous rangeland and 26.3% (s^2 = 4.2%) of their time at den sites on fragmented agriculture/rangeland. Females spent 66.8% (s^2 = 14.9%) of their time at den sites on continuous rangeland and 61.3% (s^2 = 0.7%) of their time at den sites on fragmented agriculture/rangeland.

Swift Fox pups were born 6 April – 14 April. Den site activity stations were started immediately following determination of presence of pups (Sherman County dens: 9 April 2000, 9 April 2001; Rita Blanca dens: 6 April 2000, 14 April 2001) and run until early June (Table 1). Visual observations confirmed estimated whelping dates through documentation of emergence of pups in early May (Rita Blanca dens: 7 May 2000, 9 May 2001; Sherman County dens: 5 May 2000, 6 May 2001).

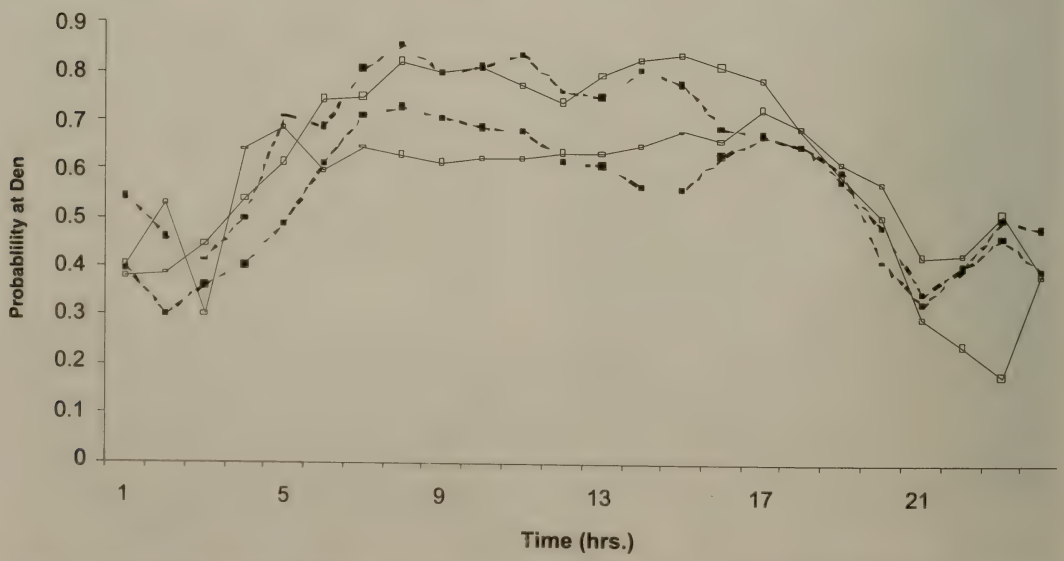


FIGURE 1. Probability of finding individual radio-collared female Swift Foxes at dens on an hourly basis based on individual dens in northwest Texas during pup rearing season (April – June), 2000 and 2001.

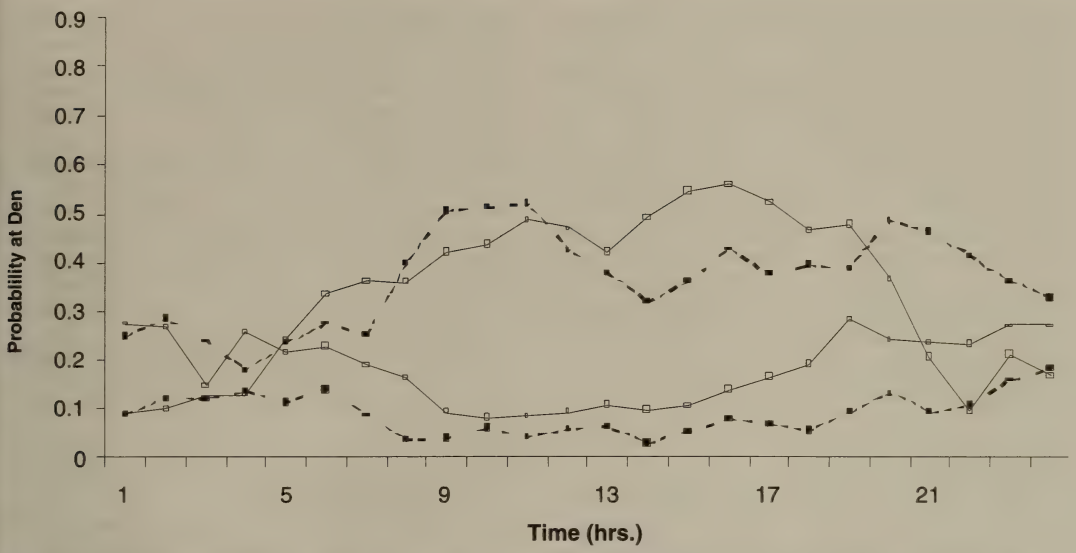


FIGURE 2. Probability of finding individual radio-collared male Swift Foxes at dens on an hourly basis based on individual dens in northwest — Texas during pup rearing season (April – June), 2000 and 2001.

Swift Fox litter sizes averaged 3.5 pups (range 2–5, n = 4). In 2000, both monitored fox pairs successfully raised all pups from 4 to 8 weeks of age (2000 Rita Blanca den: 5 pups; 2000 Sherman County den: 2 pups). In 2001, the Sherman County den raised 3 pups from 4 to 8 weeks of age. In 2001 4 pups emerged from the Rita Blanca den in 2001. However, the male was killed (11 May 2001) by Coyotes and the female died (19 May 2001) from a vehicle collision. On 23 May 2001, one pup was observed running within 150 m of the den, but no other observations of pups were made and we assumed the remaining pups died.

Following depredation of the male, the female spent 29.2% less time at the den when comparing the final 8 days (47.7%) to the first 4 weeks (76.9%) of occupation.

Discussion

During the pup-rearing season, male and female Swift Foxes were active away from dens primarily during crepuscular and nocturnal hours. However, this pattern of behavior was more distinct for females than males. Differences were documented between amount of time male (24.3%) and female (63.1%) Swift Foxes spent at den sites. Overall, females spent 2.6 times more time at dens than males during the pup-rearing season. Impacts of unequal parental care in Swift Foxes are unknown. Since males and females contribute to pup rearing, losses of either parent could have consequences for pup survival.

However, despite unequal parental care, males likely make important contributions to successful pup rearing. In Colorado, loss of a male parent resulted in a decrease in the number of pups that survived to emergence from a Swift Fox den (Covell 1992). This same phenomenon has been documented in several bird species when removal of males during nesting season resulted in decreased reproductive success (Krebs and Davies 1993). Furthermore, the importance of males to reproductive success likely increased when food resources were scarce (Krebs and Davies 1993). Although our sample size was small, our data suggested a similar pattern. Following the loss of the male parent at the Rita Blanca den during 2001, the amount of time spent at the den by the remaining female declined by 29.2%. This was probably the result of decreased food availability to pups following loss of the male, causing the female to spend more time away from the den searching for food.

Numerous studies have documented the direct impacts of Coyote depredation on Swift Fox populations (Hines 1980; Covell 1992; Carbyn et al. 1994; Sovada et al. 1998; Kitchen et al. 1999. The increased Coyote densities following removal of large predators (i.e., wolves) throughout the range of the Swift Fox may have impacted Swift Fox populations indirectly. Covell (1992) suggested that Coyote reduction increased the proportion of helpers (i.e., non-breeding adult females assisting in rearing of young) found in Swift Fox family groups. We documented two trios prior to whelping, and neither successfully whelped due to Coyote depredation within the trio. Several studies have suggested that presence of helpers in family groups increased pup survivorship (Macdonald 1979, 1983). Our results show, however that depredation by Coyotes in Swift Fox family groups may indirectly result in a decrease in success of

whelping or decreased pup survival and therefore, recruitment.

Our study suggested that Coyotes have indirect effects on success of reproduction in Swift Fox populations. Our study documented 23.5% (4 of 17) of potentially breeding females successfully raised pups to eight weeks of age. Of the remaining potentially breeding females, 70.6% (n = 12) did not whelp pups due to high mortality rates documented in this study, and 5.9% (n = 1) lost the entire litter due to depredation of the male parent and the following mortality of the female parent during pup rearing. Importance of understanding direct and indirect effects of Coyotes on Swift Fox populations may aid in determining causes of depressed Swift Fox populations.

Management Implications

High mortality rates directly, as well as indirectly, affect Swift Fox populations. High mortality of Swift Foxes in this study resulted in indirect losses of Swift Foxes through decreased breeding and pup rearing success. Control of Coyotes particularly during times preceding and during the breeding season may help improve Swift Fox reproductive success. Control may directly enhance populations of Swift Fox through decreased Coyote depredation (Kamler et al. 2003), but also may increase breeding pairs, breeding success, and pup rearing success, therefore increasing recruitment of Swift Foxes.

Acknowledgments

This project was funded by Texas Tech University, Texas Parks and Wildlife Department, United States Forest Service, Northern Prairie Wildlife Research Center, the United States Department of Agriculture's Wildlife Services program, National Fish and Wildlife Foundation, the Zoological Society of Houstson, and a Section 6 Grant E-1-12 from the U. S. Fish and Wildlife Service Endangered Species Program. Kansas Department of Wildlife and Parks and BWXT Pantex loaned us equipment. We thank the many landowners in Sherman and Dallam counties that allowed us to conduct research on their land. A special thanks goes to F. Pronger, who contacted us about Swift Foxes, then allowed us to use his ranch as a second study site. Our research protocol, number 00979BX, was approved by the Texas Tech University Animal Care and Use Committee. This is Texas Tech University, College of Agricultural Sciences and Natural Resources technical publication T-9-932.

Literature Cited

Carbyn, L. N., H. J. Armbruster, and **C. Mamo.** 1994. The Swift Fox reintroduction program in Canada from 1983 to 1992. Pages 247-271 *in* Restoration of endangered species: conceptual issues, planning and implementation. *Edited by* M. L. Bowles and C. J. Whelan. Cambridge University Press, Cambridge, United Kingdom.

Covell, D. F. 1992. Ecology of the Swift Fox (*Vulpes velox*) in southeastern Colorado. Thesis. University of Wisconsin, Madison, Wisconsin, USA.

Daan, S., C. Deerenberg, and **C. Dijkstra.** 1996. Increased daily work precipitates natural death in the kestrel. Journal of Animal Ecology 65: 539-544.

Egoscue, H. J. 1979. *Vulpes velox*. Mammalian Species 122: 1-5.

Gustafsson, L., and **W. J. Sutherland.** 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis*. Nature 335: 813-815.

Hines, T. D. 1980. An ecological study of *Vulpes velox* in Nebraska. Thesis, University of Nebraska, Lincoln, Nebraska, USA.

Kamler, J. F, W. B. Ballard, R. L. Gilliland, P. R. Lemons II, and **K. Mote.** 2003. Impacts of coyotes on swift foxes in northwestern Texas. Journal of Wildlife Management 67: 317-323.

Kilgore, D. L. 1969. An ecological study of the Swift Fox (*Vulpes velox*) in the Oklahoma Panhandle. American Midland Naturalist 81: 512-533.

Kitchen, A. M., E. M. Gese, and **E. R. Schauster.** 1999. Resource partitioning between Coyotes and Swift Foxes: space, time, and diet. Canadian Journal of Zoology 77: 1645-1656.

Koopman, M. E., B. L. Cypher, and **J. H. Scrivner.** 2000. Dispersal patterns of San Joaquin kit foxes (*Vulpes macrotis mutica*). Journal of Mammalogy 81: 213-222.

Krebs, J. R., and **N. B. Davies.** 1993. An introduction to behavioural ecology. Third edition. Blackwell Science, Oxford, United Kingdom.

Krebs, J. R., and **N. B. Davies.** 1998. Behavioural ecology: an evolutionary approach. Fourth Edition. Blackwell Science, Oxford, United Kingdom.

Macdonald, D. W. 1979. 'Helpers' in fox society. Nature 282: 69-71.

Macdonald, D. W. 1983. The ecology of carnivore social behaviour. Nature 301: 379-384.

Macdonald, D. W., and **P. D. Moehlman.** 1983. Cooperation, altruism, and restraint in the reproduction of carnivores. Pages 433-467 *in* Perspectives in ethology. *Edited by* P. Bateson and P. Klopfer. Plenum Press, New York, USA.

Moehlman, P. D. 1979. Jackal helpers and pup survival. Nature 277: 382-383.

Moehlman, P. D. 1989. Intraspecific variation in canid social systems. Pages 143-163 *in* Carnivore behavior, ecology, and evolution. *Edited by* J. L. Gittleman. Volume 1. Cornell University Press, Ithaca, New York, USA.

National Oceanic and Atmospheric Administration. 2000. Annual climatological summary. National Climatic Data Center, Asherville, North Carolina, USA.

National Oceanic and Atmospheric Administration. 2001. Annual climatological summary. National Climatic Data Center, Asherville, North Carolina, USA.

Norris, K., M. Anwar, and **A. F. Read.** 1994. Reproductive effort influences the prevalence of haematozoan parasites in great tits. Journal of Animal Ecology 63: 601-610.

Richner, H., P. Christie, and **A. Oppliger.** 1995. Paternal investment affects prevalence of malaria. Proceedings of the National Academy of Sciences of the USA 92: 1192-1194.

Samuel, D. E., and **B. B. Nelson.** 1992. Foxes (*Vulpes vulpes* and allies). Pages 485-490 *in* Wild mammals of North America. *Edited by* J. A. Chapman and G. A. Feldhamer. Johns Hopkins University Press. Baltimore, Maryland, USA.

Scott-Brown, J. M., S. Herrero, and **J. Reynolds.** 1987. Swift Fox. Pages 432-441 *in* Wild furbearer management and conservation in North America. *Edited by* M. Nowak, J. A. Baker, M. E. Obbard, and B. Malloch. Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Sovada, M. A., C. C. Roy, J. B. Bright, and **J. R. Gillis.** 1998. Causes and rates of mortality of Swift Foxes in western Kansas. Journal of Wildlife Management 62: 1300-1306.

Spiegel, L. K., and **J. Tom.** 1996. Reproduction of San Joaquin kit fox in undeveloped and oil-developed habitats of Kern County, California. Pages 53-69 *in* Studies of the San Joaquin kit fox in undeveloped and oil-developed areas. *Edited by* L. K. Spiegel. California Energy Commission, Sacramento, California, USA.

Sterns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, United Kingdom.

Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136-179 *in* Sexual selection and the descent of man 1871-1971. *Edited by* B. Campbell. Aldine, Chicago, Illinois, USA.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100: 687-690.

Zar, J. H. 1999. Biostatistical Analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Received 23 January 2002
Accepted 2 January 2004

Energy Cost of Running in an Arctic Fox, *Alopex lagopus*

EVA FUGLEI[1] and NILS A. ØRITSLAND[2]

[1]Norwegian Polar Institute, N-9296 Tromsø, Norway
[2]Outhere AS, 1361 Osteraas, Norway

Fuglei, Eva, and Nils A. Øritsland. 2003. Energy cost of running in an Arctic Fox, *Alopex lagopus*. Canadian Field-Naturalist 117(3): 430–435.

This work was conducted to determine effect of season and starvation on metabolic rate during running in the Arctic Fox (*Alopex lagopus*) on Svalbard (78°55'N, 11°56'E), Norway. Indirect calorimetry was used to measure metabolic rate of foxes running on a treadmill and heart rate was monitored using implanted radio transmitters. The relationship between heart rate and metabolic rate was also examined. Metabolic rate increased with running speed. In July the metabolic rate during running almost fitted general equations predicted for mammals, while it was up to 20% lower in January, indicating seasonal variation in metabolic rate. There was a significant positive linear relationship between heart rate and weight specific metabolic rate, suggesting that heart rate can be used as an indicator of metabolic rate. Starvation for 11 days decreased the net cost of running by 13% in January and 17% in July, suggesting that a starved fox runs more energetically efficient than when fed. Heart rate measured in July decreased by 27% during starvation. Re-feeding reversed the starvation-induced reduction in metabolic rate and heart rate during running almost up to post-absorptive levels. The present results are from one fox, and must be considered as preliminary data until further studies are conducted.

Key Words: Arctic Fox, *Alopex lagopus*, heart rate, metabolic rate, net cost of running, starvation, Svalbard.

The Arctic Fox (*Alopex lagopus*) is the only resident terrestrial carnivorous mammal in the high Arctic Svalbard archipelago (74° N-81 °N). Here, they experience extreme contrasts in light and temperature, and periodic limitations of food availability (Fuglei 2000). Therefore, physiological adaptations to seasonal variations in ambient conditions and to periods of reduced food supplies must be important for the survival of this small-sized species. The Arctic Fox moves great distances, up to 2300 km, during seasonal migrations and in search for food, and also across the pack ice (Pulliainen 1965). Fox tracks have even been observed close to the North Pole (Nansen 1897). One Arctic Fox, live trapped and ear tagged in Ny-Ålesund, Svalbard (78° 55' N, 11° 56' E), was shot on the island of Novaya Zemlya (ca. 75 °N, 55 °E; personal communication K. Frafjord and P. Prestrud), a direct line distance of about 1200 km, and the real distance traveled must have been considerably longer.

Food items are scarce during the dark winter season, and during such periods the Arctic Fox faces a conflict between the need to conserve energy and the need to actively search for food. Studies on the effect of starvation on the energy cost of running have not been carried out for the Arctic Fox and a consistent pattern of such effects has not emerged from studies of other homeotherms. For the resting state, starvation-induced reduction of basal metabolic rate (BMR), also called metabolic depression, has been found in humans (Keys et al. 1950), laboratory Wistar rats (Fuglei and Øritsland 1999a; Kleiber 1975) and also in wild species such as the Emperor Penguin (*Aptenodytes forsteri*; Dewasmes et al. 1980) and the Arctic Fox (Fuglei and Øritsland 1999b; Prestrud 1982). This adaptation is of importance because it acts to reduce the rate of body weight loss and therefore increase the chances for surviving periods of starvation. Compared to post-absorptive conditions, the net costs of running were unchanged in semi-starved humans (Joffe et al. 1919), starved dogs (Lusk 1916-17), Emperor Penguins (Dewasmes et al. 1980) and laboratory Wistar rats (Fuglei and Øritsland 1999a). The net cost of running is a measure of efficiency and is conventionally expressed as the energy needed for moving 1 kg a distance of 1 m (Dewasmes et al. 1980; Taylor et al. 1970). Thus, an unchanged net cost of running indicates no changes in energetic efficiency during exercise. In contrast, the net cost of walking decreased with semi-starvation in humans (Keys et al. 1950). Heart rate (HR) has been proposed as an indicator of metabolic rate in mammals (Lund and Folk 1976; Nilssen et al. 1984), and in birds (Bevan et al. 1994), but such data are not available for the Arctic Fox.

This work was conducted to determine the effect of season and starvation on metabolic rate and HR during running in the Arctic Fox. Additionally we wanted to examine whether HR can be used as an index of metabolic rate in the Arctic Fox.

Methods

Animals

This work was performed on Svalbard, Norway, in Ny-Ålesund (78° 55' N, 11° 56' E), at the Norwegian Polar Institute's Research Station. One male Arctic Fox was caught and held year round in an outdoor wire mesh-netting cage (2.5 m long × 2 m wide × 2 m

high), equipped with a wooden sleeping box (0.5 m long × 0.5 m wide × 1 m high). The fox was fed *ad libitum* with commercial dry fox food (FK-Revepellets, manufactured by Felleskjøpet, Norway) softened in water. Water was always provided *ad libitum*. Freezing of the food and water was prevented during the winter by use of thermostatically controlled heating elements in the feeding cup.

Metabolic rate

Detailed descriptions of the apparatus and methods used to measure oxygen consumption and carbon dioxide production, and the calculation of metabolic rate are described elsewhere (Fuglei and Øritsland 1999a, b). Briefly, metabolic rate during running was measured in an open-circuit system, composed of a treadmill located inside a plexiglas respiratory chamber (101 cm long × 38 cm wide × 50 cm high) in a climate chamber. BMR (IUPS Thermal Commission, 2001) was measured in the same system using a plexiglas respiratory chamber (41 cm long × 41 cm wide × 41 cm high; for details see Fuglei and Øritsland 1999b). Oxygen concentration was determined using an oxygen analyzer (S-3A, R-1 and N-22M, Applied Electrochemistry Inc., Sunnyvale, California). A carbon dioxide analyzer (Binos-100, Rosemount GmbH & Co, Hanau, Germany) was used to determine carbon dioxide. Chamber airflow, which was maintained at 33.0 $l \cdot min^{-1}$ when measuring metabolic rate during running and at 10.0 $l \cdot min^{-1}$ when measuring BMR using a Charles Austen Pump (B100 DEC, England), was monitored using a mass flow meter (Bronkhorst Hi-tec, Vorde, Holland) with a control valve (F 113-EA-55-V) and a readout system (E-5514-FA). Values for oxygen consumption and carbon dioxide production were determined from the difference in the concentration of the air entering and leaving the chamber, and from the rate of airflow through the chamber. Metabolic rate was expressed as watts per kg body weight.

BMR was subtracted from metabolic rate during running in order to focus exclusively on the net cost of running (Dewasmes et al. 1980; Fuglei and Øritsland 1999a). Thus the net cost of running was calculated from the equation:

[1] $M_N = (M_{run} - BMR) \cdot v^{-1}$

where M_N is the net cost of moving 1 kg a distance of 1 m ($J \cdot m^{-1} \cdot kg^{-1}$), M_{run} is metabolic rate during running ($J \cdot s^{-1} \cdot kg^{-1}$), BMR is basal metabolic rate ($J \cdot s^{-1} \cdot kg^{-1}$), and v is speed ($m \cdot s^{-1}$).

Heart rate

The HR transmitter was surgically implanted in April 1997. The fox was fasted for 12 h before surgery and then anaesthetized with a mixture of medetomidine (Domitor® Orion Corporation Animal Health, Turku, Finland; 0.05 mg/kg) and ketamine (Parke-Davis; 3 mg/kg). The HR transmitter (DataCol 5.0, Mini Mitter, Oregon, USA, model VHF-C-1) was 6.3 cm × 2.3 cm and weighed 44 g, approximately 1.5% of the body weight. The HR transmitter was inserted in the abdominal cavity through a ventral midline incision. The two HR electrodes exited the abdominal cavity. One was placed under the skin above the sternum and the other was positioned on the inside of the left foreleg pit via a subdermal tunnel. A more detailed description of the operational procedure is presented elsewhere (Fuglei et al. 2002). The fox was kept indoors in a small cage for 1-2 days until recovery, and inspected regularly. All training and experiments were conducted at least 1-2 months after surgical implantation of the transmitter. Each HR value was the average of 10 heartbeats.

Experimental protocol

Experiments were conducted in the winter and summer season during 24-h darkness in January 1997, and 24-h daylight in July 1997. In January metabolic rate was measured in one post-absorptive, then starved and then re-fed fox, and the same was measured in July, but then simultaneously with HR. Mean air temperature in the metabolic chamber was -3 ± 3 °C in January and 9 ± 1 °C in July. When not engaged in the experiments, the animal was exposed to ambient temperatures in the outdoor holding cage averaging -18 °C in January and 3 °C in July. These temperatures are considered to be within the thermoneutral zone of winter and summer adapted Arctic Foxes (Casey et al. 1979; Underwood 1971). The fox was trained for the exercise experiment daily for three weeks, at three different running speeds: 3.9, 4.8 and 5.8 $km \cdot h^{-1}$ (1.08, 1.33 and 1.61 $m \cdot s^{-1}$). Metabolic rate in the post-absorptive, starved and re-fed state were measured between 08:00-12:00 h both in January and July. To ensure post-absorptive, pre-starvation conditions, food was withdrawn 12-h prior to the experiments (day 1). Then, measurements were taken at each speed over several days in January (3.9 $km \cdot h^{-1}$, n = 3; 4.8 $km \cdot h^{-1}$, n = 4; 5.8 $km \cdot h^{-1}$, n = 2) and in July (3.9 $km \cdot h^{-1}$, n = 8; 4.8 $km \cdot h^{-1}$, n = 6; 5.8 $km \cdot h^{-1}$, n = 6). During the starvation experiments, only two speeds were used, 3.9 $km \cdot h^{-1}$ and 5.8 $km \cdot h^{-1}$. The fox starved for 11 days, both in January and July. During re-feeding for four additional days, the fox was fed *ad libitum*. The fox was weighed using a spring scale (Pesola 0-10 kg) with an accuracy of ± 0.1 kg.

Statistics

Repeated measurements of post-absorptive metabolic rates and HR during running, 4-10 days before initiating starvation experiments, were expressed as means ± SD. The relationship between post-absorptive metabolic rate and HR were tested with linear regression (PROCLIN, SAS).

Results

After 11 days of starvation, the body weight of the Arctic Fox held in captivity under ambient conditions decreased to 81% of its initial body weight of 4.05 kg in January, and to 75% of initial body weight of 3.66 kg

in July. After four days of re-feeding, the body weight increased to 93% of its initial level in January and to 89% in July.

Post-absorptive metabolic rate during running increased linearly with increasing speed. In July the metabolic rate while running almost fitted general equations predicted for mammals (Taylor et al. 1982; equation 2) relating metabolic rate at a constant speed to speed and body weight, while it was up to 20% lower in January (equations 3 and 4).

[2] Metabolic rate = $10.7 \cdot BW^{-0.316} \cdot v + 6.03 \cdot BW^{-0.303}$,

where metabolic rate is $W \cdot kg^{-1}$, BW is body weight in kg, and v is speed in $m \cdot s^{-1}$. The calculated metabolic rate during running gave the following formula for the fox when it weighed 4.05 kg in January:

[3] Metabolic rate = $6.88 \cdot v + 3.95$,

and for the fox when it weighed 3.66 kg in July:

[4] Metabolic rate = $7.10 \cdot v + 4.07$

The post-absorptive metabolic rate while running was up to 14% lower in January compared to July (equations 5 and 6, Figure 1).

[5] M_{run} in January = $3.23 \cdot v + 6.97$ ($n = 9$; $r^2 = 0.80$)

[6] M_{run} in July = $2.63 \cdot v + 9.38$ ($n = 20$; $r^2 = 0.71$),

where M_{run} is metabolic rate during running in $W \cdot kg^{-1}$ and v is speed in $m \cdot s^{-1}$.

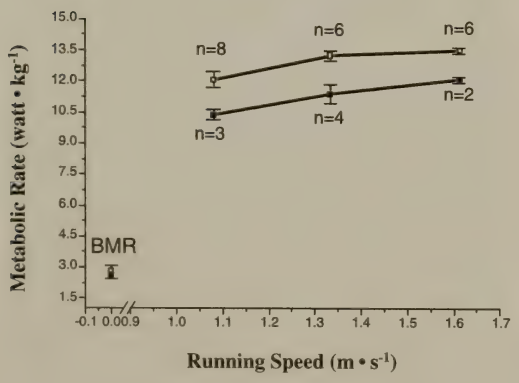


FIGURE 1. Post-absorptive basal metabolic rate (BMR; $W \cdot kg^{-1}$) and metabolic rate in one Arctic Fox running on a treadmill at three different speeds in January (solid squares) and in July (open squares) (n = the number of experiments). The equations describing the relationships between metabolic rate and running speeds are: Metabolic rate in January = $3.23 \cdot v + 6.97$ ($n = 9$; $r^2 = 0.80$); Metabolic rate in July = $2.63 \cdot v + 9.38$ ($n = 20$; $r^2 = 0.71$).

Conventionally, the net cost of running is expressed as the energy needed for moving 1 kg a distance of 1 m, also referred to as the efficiency of locomotion (Dewasmes et al. 1980; Fuglei and Øritsland 1999a). In the post-absorptive Arctic Fox, the net cost of running was about 15% lower in January compared to July (Table 2). HR, which was measured only in July, increased with running speed (Figure 2). There was a significant positive linear relationship between HR and metabolic rate at increasing running speeds (Figure 3). The equation describing the relationship between the two variables is:

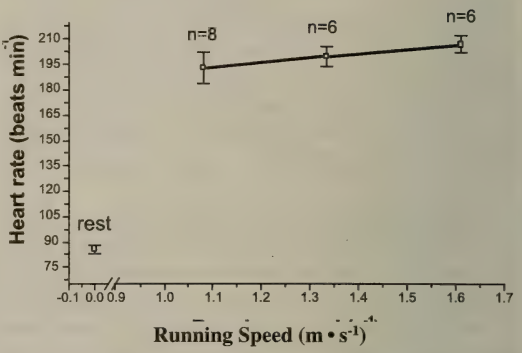


FIGURE 2. Post-absorptive mean heart rate (bpm) in one Arctic Fox running on a treadmill at three different speeds in July (n = the number of experiments).

[7] Metabolic rate = $-5.18 + 0.09 \cdot HR$ ($n = 19$; $r^2 = 0.98$; $p < 0.0001$),

where metabolic rate is in $W \cdot kg^{-1}$ and HR is beats $\cdot$ min^{-1}.

Starvation for 11 days induced a reduction in metabolic rate during running, with up to 11% lower values in January and 14% in July (Table 1a). Starvation for 11 days decreased the net cost of running from post-absorptive values by up to 13% in January, and 17% in July (Table 2). HR measured in July decreased after 11 days starvation by up to 27% at different running speeds (Table 1a).

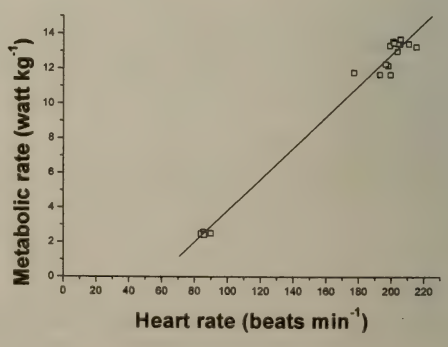


FIGURE 3. Basal metabolic rate and metabolic rate while running on a treadmill ($W \cdot kg^{-1}$) at three different speeds as a function of heart rate (HR; bpm) in one Arctic Fox. The regression equation is: Metabolic rate = $-5.18 + 0.09$ HR ($r^2 = 0.98$, $p < 0.0001$).

TABLE 1a. Metabolic rates during running (M_{run}; $W \cdot kg^{-1}$) at two speeds 3.9 and 5.8 km $\cdot h^{-1}$ of one Arctic Fox when in a post-absorptive state (day 1) and during starvation (day 3-11) in January and July. Heart rate (HR) in beats per min (bpm) was monitored only in July. Several experiments were conducted on the post-absorptive fox (day 1), as indicated by SD values and the number of experiments in parenthesis.

	January		July			
	3.9 km $\cdot h^{-1}$	5.8 km $\cdot h^{-1}$	3.9 km $\cdot h^{-1}$		5.8 km $\cdot h^{-1}$	
Days	M_{run} ($W \cdot kg^{-1}$)	M_{run} ($W \cdot kg^{-1}$)	M_{run} ($W \cdot kg^{-1}$)	HR (bpm)	M_{run} ($W \cdot kg^{-1}$)	HR (bpm)
1	10.38 ± 0.27 (n = 3)	12.07 ± 0.13 (n = 2)	12.07 ± 0.41 (n = 8)	193 ± 9 (n = 8)	13.44 ± 0.14 (n = 6)	207 ± 5 (n = 6)
3	9.76	11.54	11.14	181	12.36	199
5	9.66	11.68	10.72	175	12.18	192
7	9.11	10.84	10.49	165	12.21	185
9	9.32	11.29	10.51	147	12.06	175
11	9.36	10.74	10.36	140	12.05	163

TABLE 1b. Metabolic rates during running (M_{run}; $W \cdot kg^{-1}$) at two speeds 3.9 and 5.8 km $\cdot h^{-1}$ of one Arctic Fox during 2 and 4 days of re-feeding in January and July. Heart rate (HR) was monitored in July only.

	January		July			
	3.9 km $\cdot h^{-1}$	5.8 km $\cdot h^{-1}$	3.9 km $\cdot h^{-1}$		5.8 km $\cdot h^{-1}$	
Days	M_{run} ($W \cdot kg^{-1}$)	M_{run} ($W \cdot kg^{-1}$)	M_{run} ($W \cdot kg^{-1}$)	HR (bpm)	M_{run} ($W \cdot kg^{-1}$)	HR (bpm)
2	10.98	11.80	10.30	149	12.20	169
4	9.84	11.53	10.75	176	12.00	189

TABLE 2. The net cost of running (M_N; $J \cdot m^{-1} \cdot kg^{-1}$) in one Arctic Fox in post-absorptive condition (PA) and after 11 days starvation (S) in January and July, when running at two speeds 3.9, and 5.8 km $\cdot h^{-1}$.

		January		July	
	Running speed	PA	S	PA	S
M_N ($J \cdot m^{-1} \cdot kg^{-1}$)	3.9 km $\cdot h^{-1}$	7.24	6.36	8.56	7.11
M_N ($J \cdot m^{-1} \cdot kg^{-1}$)	5.8 km $\cdot h^{-1}$	5.90	5.12	6.58	5.81

Ad libitum re-feeding for four days reversed the starvation-induced reduction in metabolic rate during running to about 96% of post-absorptive values in January, and 89% in July, while HR increased to 92% of post-absorptive values (Table 1b).

Discussion

Compared to the general formula for the metabolic cost of running in mammals (Taylor et al. 1982), the measured values in the Arctic Fox in January were as much as 20% lower, indicating that the Arctic Fox is an energetically efficient runner. Both the metabolic rate during running (Figure 1) and the net cost of running (Table 2) were lower in January compared to July. A seasonal trend in post-absorptive BMR in Arctic Foxes, with 11-15% lower values in winter than in summer, is suggested to be a physiological adaptation important for energy conservation during winter (Fuglei and Øritsland 1999b). Thus, the present study supports the indication of a physiological adaptation aiding energy conservation during winter in Arctic Foxes. This may be important for food searching and therefore survival.

The metabolic cost of running in the herbivorous Svalbard Reindeer (*Rangifer tarandus platyrhynchus*) is reported to fit the values predicted by the equation of Taylor et al. (1982) within 3% (Nilssen et al. 1984). Another inhabitant of the Arctic, the carnivorous Polar Bear (*Ursus maritimus*), is in contrast to the Arctic Fox considered to be an inefficient runner (Hurst et al. 1982; Øritsland et al. 1976). The Arctic Fox and the Polar Bear have some similar behavior patterns; i.e. both species wander great distances in search for food during seasonal migrations. Humans excepted, they lack natural enemies, and Polar Bears break the snow cover over subnivean birth lairs of Ringed Seals (*Phoca hispida*) when hunting for pups (Lydersen and Gjertz 1986; Smith 1980). However, the Arctic Fox is much smaller, has an unfavorable higher surface-volume ratio, and is adapted to terrestrial life. Thus, its star-

vation survival capacity during rest is relatively poor, and the energetically efficient locomotion indicated by the present work may be important for still keeping active searching for food.

There was a clear linear relationship between HR and metabolic rate during increasing running speed (Figure 3). To develop a representative equation for the relationship between HR and metabolic rate that can be used to estimate metabolic rate in free-living Arctic Foxes, further studies must be conducted on several individuals running over a wider range of speeds.

The starvation-induced decrement of BMR previously found in Arctic Foxes (Fuglei and Øritsland 1999b; Prestrud 1982) appears to be maintained during running in that metabolic rates during running were 10-11% lower than those during the post-absorptive states in January and July (Table 1a). Furthermore, the net cost of running decreased during starvation (Table 2). Also HR was reduced by up to 27% (Table 1a), indicating an energetically increased efficiency in the starved Arctic Fox when running. This increased efficiency when running during starvation is consistent with earlier studies on humans (Keys et al. 1950), and in Emperor Penguins below a specific body weight (Dewasmes et al. 1980). It is interesting to note that the net cost of running decreased with increasing running speed (Table 2). In general, the cost of moving 1 kg a distance of 1 m is independent of speed (Fancy and White 1985). However, the relationship between increasing metabolic rate and running speed has been described as a series of curvilinear relationships (Fancy and White 1985). This means that the total cost per m declines curvilinearly with increasing speed until a minimal asymptotic cost per m is achieved (Fancy and White 1985; Taylor et al. 1970). Regarding the present study, the differences between the running speeds were low and may be within the curvilinearity mentioned above, and had not yet reached the minimal asymptotic cost at that gait.

The reversion of metabolic rate and heart rate during re-feeding (Table 1b) demonstrates that the starvation-induced decrease of the variables was not a training effect, and thus validates the present results.

Conclusions: Both post-absorptive metabolic rate during running and the net cost of running were lower in winter compared to summer, which implies that the Arctic Fox may be an energetically efficient runner during the season when food is least available. HR can be used as an indicator of metabolic rate in the Arctic Fox. Starvation for 11 days reduced metabolic rate during running and the net cost of running, suggesting that the Arctic Fox appears to run in a more energetically efficient manner when starved. This may be important for survival when the food is limited. The present results are from one fox, and must be considered as preliminary data until further studies are conducted.

Acknowledgments

We are grateful to E. Moldstad who built and improved the treadmill several times. We thank J. B. Mercer for help with the surgical implantation of the HR transmitter and for valuable comments on the manuscript. We thank J. B. Steen and E. P. Pierce for comments on the manuscript. The Governor of Svalbard and Kings Bay A/S gave the permission to capture the fox that was used in this project. The Arctic Fox was cared for in accordance with the principles and guidelines of the Norwegian Animal Welfare Act, under permission from the National Animal Research Authority.

Literature Cited

Bevan, R. M., A. J. Woakes, P. J. Butler, and **I. L. Boyd.** 1994. The use of heart rate to estimate oxygen consumption of free-ranging black-browed albatrosses. Journal of Experimental Biology 193: 119-137.

Casey, T. M., P. C. Withers, and **K. K. Casey.** 1979. Metabolic and respiratory responses of arctic mammals to ambient temperature during summer. Comparative Biochemistry and Physiology 64A: 331-341.

Dewasmes, G., Y. Le Maho, A., Cornet, and **R. Groscolas.** 1980. Resting metabolic rate and cost of locomotion in long-term fasting emperor penguins. Journal of Applied Physiology 49: 888-896.

Fancy, S. G., and **R. G. White.** 1985. Incremental cost of activity. Chapter 7, pages 143-159 *in* Bioenergetics of Wild Herbivores. *Edited by* R. J. Hudson and R. G. White. CRC Press, Inc., Boca Raton.

Fuglei, E. 2000. Physiological adaptations of the arctic fox to high Arctic conditions. Ph.D. dissertation, University of Oslo, Oslo, Norway.

Fuglei, E., and **N. A. Øritsland.** 1999a. Body composition, resting and running metabolic rates, and net cost of running in rats during starvation. Acta Physiological Scandinavica 165: 203-210.

Fuglei, E., and **N. A. Øritsland.** 1999b. Seasonal trends in body mass, food intake and resting metabolic rate, and induction of metabolic depression in arctic foxes (*Alopex lagopus*) at Svalbard. Journal of Comparative Physiology B 169: 361-369.

Fuglei, E., J. B. Mercer, and **J. M. Arnemo.** 2002. Surgical implantation of radio transmitters in arctic foxes (*Alopex lagopus*) on Svalbard, Norway. Journal of Zoo and Wildlife Medicine 33(4): 342-349.

Hurst, R. J., M. L. Leonard, P. D. Watts, P. Beckerton, and **N. A. Øritsland.** 1982. Polar bear locomotion: body temperature and energetic cost. Canadian Journal of Zoology 60: 40-44.

IUPS Thermal Commission. 2001. Glossary of terms for thermal physiology. The Japanese Journal of Physiology 51(2): 245-280.

Joffe, J., E. P. Poulton, and **J. H. Ryffel.** 1919. The respiratory metabolism in a case of prolonged undernutrition. Quarterly Journal Medicine 12: 334-346.

Keys, A., J. Brozek, A. Henschel, O. Michelsen, and **H. L. Taylor.** 1950. The Biology of Human Starvation. Volume 1. The University of Minnesota Press, Minneapolis, Minnesota. 763 pages.

Kleiber, M. 1975. The fire of life: An introduction to animal energetics. Robert E. Krieger Publishing Company, Inc. Malabar, Florida. 453 pages.

Lund, G. F., and **G. E. Folk.** 1976. Simultaneous measurements of heart rate and oxygen consumption in black-tailed prairie dogs (*Cynomys ludovicianus*). Comparative Biochemistry and Physiology 55A: 201-206.

Lusk, G. 1916-17. The influence of diet on the heat production during mechanical work in the dog. Proceedings of the Society for Experimental Biology and Medicine 14: 92-93.

Lydersen, C., and **I. Gjertz.** 1986. Studies of the ringed seal (*Phoca hispida* Schreber 1775) in its breeding habitat in Kongsfjorden, Svalbard. Polar Research 4: 57-63.

Nansen, F. 1897. Farthest North. The Norwegian Polar Expedition 1893-1896. Archibald Constable and Company, Whitehall Gardens. Volume 1-2. 1181 pages.

Nilssen, K. J., H. K. Johnsen, A. Rognmo, and **A. S. Blix.** 1984. Heart rate and energy expenditure in resting and running Svalbard and Norwegian reindeer. American Journal of Physiology 246: R963-R967.

Øritsland, N. A., C. Jonkel, and **K. Ronald.** 1976. A respiration chamber for exercising polar bears. Norwegian Journal of Zoology 24: 65-67.

Prestrud, P. 1982. Årstidvariasjoner i basalmetabolisme og fettlagring hos fjellreven (*Alopex lagopus*) på Svalbard (Seasonal variations in basal metabolic rate and fat deposition of the arctic fox (*Alopex lagopus*) in Svalbard). Cand real thesis, University of Oslo, Norway, [In Norwegian] 95 pages.

Pulliainen, E. 1965. On the distribution and migrations of the arctic fox (*Alopex lagopus* L.) in Finland. Aquilo Serie Zoologica 2: 25-40.

Smith, T. G. 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Canadian Journal of Zoology 58: 2201-2209.

Taylor, C. R., K. Schmidt-Nielsen, and **J. L. Raab.** 1970. Scaling of energetic cost of running to body size in mammals. American Journal of Physiology 219: 1104-1107.

Taylor, C. R., N. C. Heglund, and **G. M. O Maloiy.** 1982. Energetics and mechanics of terrestrial locomotion. Journal of Experimental Biology 97: 1-21.

Underwood, L. S. 1971. The bioenergetics of the arctic fox (*Alopex lagopus* L.). Ph.D. thesis, Pennsylvania State University. 85 pages.

Received 7 March 2002
Accepted 18 February 2004

Population Structure, Growth, and Age Estimation of Spotted Turtles, *Clemmys guttata*, Near their Northern Limit: an 18-Year Follow-up

David C. Seburn

Seburn Ecological Services, 920 Mussell Road, RR#1 Oxford Mills, Ontario K0G 1S0 Canada

Seburn, David C. 2003. Population structure, growth, and age estimation of Spotted Turtles, *Clemmys guttata*, near their northern limit: an 18-year follow-up. Canadian Field-Naturalist 117(3): 436–439.

Mark-recapture and radio telemetry data were collected from 1999-2001 on a population of Spotted Turtles, *Clemmys guttata*, near their northern limit in Ontario, Canada, and compared with a similar study conducted from 1983-1986. In 1999-2001, 32 Spotted Turtles were caught, 27 of which were adults. Females outnumbered males 3.5:1. The carapace length (CL) of adult males (108.5 ± 5.7 mm) and adult females (106.4 ± 6.0 mm) did not differ significantly. A minimum of 22% of juveniles and 40% of adults marked in 1983-1984 were still alive in 1999-2001. Adult population size was estimated to be 45 (95% confidence interval: 34-78). The average size of individual adults marked in 1983 (105.6 ± 6.0 mm CL) and recaptured during 1999-2001 (106.3 ± 5.9 mm CL) did not differ significantly. There was also no signficant difference in the number of growth lines on adults caught in 1983 (12.9 ± 2.0) and 1999 (14.0 ± 2.3). Based on the number of growth lines in 1983, these turtles averaged a minimum of 28.9 years in 1999, but actual ages are likely greater. Summer range length averaged 233 m (range: 200-275 m), while total range length averaged 327 m (range: 275-375 m).

Key Words: Spotted Turtle, *Clemmys guttata*, demographics, growth, home range, hibernation.

The global status of the Spotted Turtle (*Clemmys guttata*) is Vulnerable, indicating the species faces "a high risk of extinction in the medium-term future" (Hilton-Taylor 2000). In Canada, the Spotted Turtle is listed as a species of Special Concern (Oldham 1991*). Canadian populations are limited to Ontario, where populations are believed to be declining as a result of habitat loss, degradation and fragmentation, as well as collecting for the pet trade (Seburn and Seburn 2000).

Spotted Turtles are small (<15 cm carapace length, CL) and secretive. They frequently make use of a wide variety of habitats in wetland complexes over the course of the year (Ernst et al. 1994); however, populations in eastern Ontario appear to be limited to bogs (Cook et al. 1980). Spotted Turtles can live for over 30 years (Ernst et al. 1994), yet most studies are only a few years long (but see Litzgus and Brooks 1998a). The present study follows up on an intensive mark recapture study which resulted in 39 Spotted Turtles (9 juveniles, 12 males and 18 females) being marked in an isolated population at Mer Bleue Bog (Chippindale 1984*, 1985*). A follow-up study was undertaken to determine a current population estimate for management purposes. In addition, recapture data from turtles marked by Chippindale provide an opportunity to determine minimum survivorship and to test whether growth lines accurately reflect age.

Study Area

Research was carried out at Mer Bleue Bog, a 2500 ha sphagnum bog within the city of Ottawa, Ontario, Canada (45° 25'N, 75° 25'W). Mer Bleue Bog is owned by the National Capital Commission and public access is strictly controlled. An internationally significant wetland, Mer Bleue has been designated a Ramsar site. In the centre of the bog the peat is 3.5-6.5 m thick and it is here that five sandy islands rise through the bog mat (Brunton 1984*). Around and connecting three of the five islands are small (<1 m wide) aquatic channels. There are also a number of ponds (< 3 m in diameter) created by practice bombing during World War II. The area around the islands is open bog mat with scattered Black Spruce (*Picea mariana*) and Larch (*Larix laricina*). The islands also have Trembling Aspen (*Populus tremuloides*), Largetooth Aspen (*P. grandidentata*) and Red Maple (*Acer rubrum*) growing on them. Common plant species in the bog include sphagnum (*Sphagnum* spp.), Leatherleaf (*Chamaedaphne calyculata*), Buckbean (*Menyanthes trifoliata*), Small Cranberry (*Vaccinium oxycoccus*), and Large Cranberry (*V. macrocarpon*; Brunton 1984*).

Methods

Field studies were undertaken from 26 April 1999 until 25 May 2001, with the majority of field work concentrated in the spring and summer of 1999 and the spring of 2001. Turtles were caught by hand. Upon first capture, each turtle was weighed with a Pesola scale (± 2 g) and carapace length (CL) and width and plastron length (PL) and width were measured with vernier calipers (± 0.5 mm). The number of growth lines were counted (when possible) on the left humeral or pectoral scute of the plastron. Unmarked turtles were notched using the system used by Chippindale (Cagle 1939). The sex of adults was determined by examining secondary sex characteristics: males have a pronounced concave plastron and the vent is posterior to the carapace's edge. Raw data are on file with the

Natural Heritage Information Centre of the Ontario Ministry of Natural Resources in Peterborough.

Telemetry equipment obtained from Holohil Systems (Carp, Ontario) consisted of modified SI-2 transmitters. The transmitters were approximately 10 × 30 mm and weighed 10 g. Only turtles weighing approximately 200 g or more had transmitters attached to them. Transmitters were attached to the posterior marginal scute above the hind leg of the turtle using brass screws. Turtles were tracked using a TRX-2000S receiver and a three-element folding Yagi antenna.

Spotted Turtle movements were confined to channels within the bog, hence area was not meaningful and home range lengths were calculated. Summer range lengths were defined as the maximum straight line distance crossing the mapped observation points during May to July. Total range lengths included the hibernaculum in the calculation. Adult population size and the 95% binomial confidence interval were calculated using the program CAPTURE (Rexstad and Burnham 1992*). Size at maturity was based on the smallest turtle I caught that was first marked in 1983. This female was 97.2 mm CL and a minimum of 28 years old in 1999, based on the presence of 12 growth lines in 1983. The smallest male with obvious secondary sexual characteristics was 100.5 mm CL. Statistical analyses were conducted using MINITAB (Ryan and Joiner 1994). Although Chippindale marked 49 Spotted Turtles (Chippindale 1989) data are only available on the 39 turtles marked in 1983 and 1984 (Chippindale 1984*, 1985*). Research was conducted under the approval of the Wildlife Animal Care Committee of the Ontario Ministry of Natural Resources, protocols #99-52, 00-52, 01-52.

Results

I caught 32 Spotted Turtles, 27 of which were adults (Figure 1). The sex ratio of adults was strongly female biased (21 females to 6 males; 3.5:1; χ^2 = 8.3, p<0.005). The average CL of adult males (108.5 ± 5.7 mm, n=6) and adult females (106.4 ± 6.0 mm, n=21) did not differ significantly (t=0.79, p=0.45). Similarly, the average weight of males (187 ± 21 g, n=6) and females (192 ± 30 g, n=21) did not differ significantly (t=0.49, p=0.64). The average CL of adults from Mer Bleue (106.9 ± 5.9 mm, n=27) and elsewhere in Ontario (121.4 ± 7.4 mm n=26; Haxton 1998) differed significantly (t=7.92, p<0.0001).

The adult population size was estimated to be 45 (95% confidence interval: 34-78) using the 1999-2001 and 58 (95% confidence interval: 41-108) using Chippindale's 1983-1984 data.

Fourteen of the adults (52%) I captured were marked by Paul Chippindale in 1983. While 67% of the males caught had been previously marked, only 48% of the females were marked. I did not recapture any of the six turtles Chippindale marked in 1984. Twelve of the adults I caught were marked as adults in 1983, hence

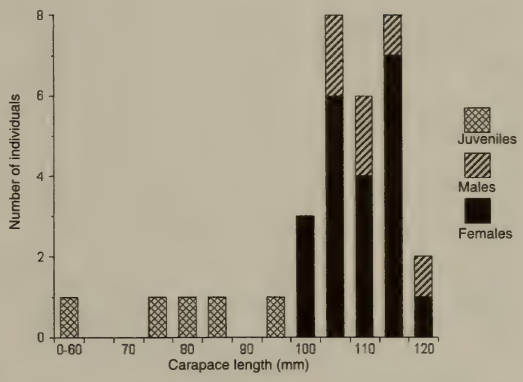


FIGURE 1. Frequency distribution of Spotted Turtles captured at Mer Bleue Bog, Ontario in 1999 and 2001.

a minimum of 40% of the adults marked in 1983-1984 were still part of the population 16 years later. In contrast, I captured only 22% of the juveniles marked by Chippindale in 1983-1984. Although the five smallest turtles Chippindale marked were not recaptured there was no statistically significant difference in the size of the turtles recaptured versus those not recaptured (W=310.0, p=0.52).

The average size of nine adults marked in 1983 (105.6 ± 6.0 mm CL) and recaptured during 1999-2001 (106.3 + 5.9 mm CL) did not differ significantly over time (t=0.28, p=0.79; Figure 2). Two juveniles captured during both time periods grew an average of 7.3 mm (Figure 2). The number of growth lines on seven adults caught in 1983 (12.9 ± 2.0) and in 1999 (14.0 ± 2.3) did not differ significantly over time (t=0.93, p=0.37). Based on the number of growth lines in 1983 and the elapsed time until they were recaptured, these turtles average a minimum of 28.9 years and one turtle was at least 33 years old. There is no reason to assume the number of growth lines in 1983 accurately reflected ages and hence it is likely that these turtles are even older.

Growth data were also collected on one yearling caught on two different occasions. On 20 May 1999, the turtle was 28.4 mm CL and 23.0 mm PL. It was recaptured 41 days later, at which time it was 33.3 mm CL and 26.8 mm PL, an increase of 0.12 mm/day CL and 0.09 mm/day PL.

I tracked one male and two females periodically during the summer and fall of 1999 using radio telemetry. The number of observations for each turtle varied from 9 to 10. Turtles appeared to remain within small aquatic channels surrounding and connecting the islands in the bog mat. Summer range length averaged 233 m (range: 200-275 m) and total range length averaged 327 m (range: 275-375 m). All three turtles hibernated outside of their summer range.

On 15 November 1999, after the turtles had entered hibernation, all three turtles bearing radio transmitters

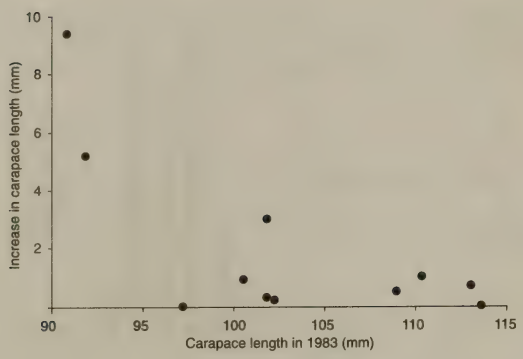


FIGURE 2. Growth of Spotted Turtles marked originally in 1983 and recaptured in 1999 or 2001 at Mer Bleue Bog, Ontario.

were tracked to the same shrubby hummock. It is highly unlikely that only Spotted Turtles with transmitters chose to overwinter in this hummock and this site likely represents a major communal hibernaculum for this population. On 10 April 2001, with some snow still on the ground, six turtles were caught in the vicinity of the known hibernaculum: one turtle was within 10 m of it, while the other five were approximately 30 m from it around another hummock. One of these turtles had overwintered at the known hibernaculum in 1999.

Discussion

Monitoring turtle populations for conservation purposes is challenging. Abundance estimates for adults alone are inadequate to determine the viability of populations given the longevity of adults, hence reproductive rates and age structures should also be monitored (Gibbs and Amato 2000). In the current study, the adult population at Mer Bleue may have declined by 20% (from 58 to 45) from 1983 to 2001, although this decline is not statistically significant. At the same time the sex ratio became increasingly female biased. Based on the population estimates and sex ratios for the two time periods, there were approximately 35 females and 23 males in 1983-1984, and 35 females and only 10 males in 1999-2001. This suggests a decline in the number of adult males; however, it is also possible that these missing males are merely undetected due to differential catchability. The confirmed presence of juveniles recruited into the adult population and the ongoing presence of juveniles is suggestive of a healthy population. Nonetheless, uncertainty remains: assuming that the 1983-1984 adult population estimate is approximately correct, then I captured roughly 47% of the adults in 1999-2001. Despite having data on roughly half of the adult population it is not possible to determine if the population has declined by 20%.

The age of turtles has often been estimated by the use of growth lines on the plastron, yet few studies have tested the validity of this method. Adults marked at Mer Bleue in 1983 showed essentially no growth or increase in the number of growth lines over 16-18 years. Similarly, Litzgus and Brooks (1998a, 1998b) found adult Spotted Turtles did not grow appreciably and that the number of growth lines added was consistently less than the number of years that had elapsed. Even in subadult turtles, growth lines are not always produced annually (Brooks et al. 1997). Hence, growth lines appear to be of little value in estimating age after maturity has been reached.

An average total home range length of 327 m is similar to mean home range lengths of 302 and 320 m for two populations of Spotted Turtles in Massachusetts (Milam and Melvin 2001). Maximum total range length in the current study was only 375 m, whereas it was over 1000 m elsewhere in Ontario (Haxton 1998) and in Massachusetts (Milam and Melvin 2001). The difference in movements is likely explained by differences in habitat. Turtles at the other sites were moving among wetlands, whereas the Mer Bleue turtles are confined to the centre of one large bog.

Spotted Turtles at Mer Bleue demonstrate fidelity to a hibernation area, however, not necessarily to the same hibernaculum. Similarly, nine Spotted Turtle hibernacula with up to 34 individuals were found in an 85 m^2 area of a fen in Ohio (Lewis and Ritzenthaler 1997). Results from the previous study at Mer Bleue suggest the known hibernation area has been used since at least the winter of 1983-1984 (Chippindale 1985*). Such fidelity to a hibernation area emphasizes the importance of certain habitats. At Mer Bleue, a circle with radius 400 m centred on the known hibernation area would enclose the activity areas of the three turtles with transmitters. Given the fact that there was very little movement of turtles among some of the islands and that turtles have been captured at other areas of the bog early in the season, it is most probable that there is more than one hibernation centre. Other studies of Spotted Turtles also support the notion of multiple hibernation centres. Individuals in one population hibernated in at least three different small bogs (Haxton and Berrill 1999), while in another population 18 hibernacula were found in five different sphagnum swamps (Litzgus et al. 1999). Effective management of Spotted Turtle populations should focus on identifying and ensuring the protection of all major hibernacula and the habitat that connects them.

Acknowledgments

I am grateful to the Ottawa Stewardship Council for coordinating this project and to the National Capital Commission for allowing me to work at Mer Bleue. Financial support in 1999 came from the Mountain Equipment Co-op, the Community Fisheries and Wild-

life Involvement Program (CFWIP) of the Ontario Ministry of Natural Resources, and the Community Environmental Grants Program (CEPGP) of the then Regional Municipality of Ottawa-Carleton. Support in 2001 was provided by the Species at Risk fund of the Ontario Ministry of Natural Resources. Special thanks to Leslie Bol for assisting with the field work in 1999. I am indebted to Paul Chippindale, whose dedicated work in the 1980s helped put my own humble efforts into a broader and more meaningful context. My deepest thanks go to Carolyn Seburn, who helped with many aspects of the project, but missed out on the fun of wading hip-deep in bog water. Francis Cook, Tim Haxton, Carolyn Seburn and two anonymous reviewers provided helpful comments on earlier drafts of this manuscript.

Documents Cited (marked * in text)

Brunton, D. F. 1984. The vegetation and flora of the Mer Bleue Conservation Area, National Capital Commission Greenbelt, Ottawa-Carleton, Ontario. Conservation Studies 22, National Capital Commission, Ottawa.

Chippindale, P. 1984. A Study of the Spotted Turtle (*Clemmys guttata*) in Mer Bleue Bog. Conservation Studies Publication Number 25, National Capital Commission, Ottawa, Ontario. 84 pages.

Chippindale, P. 1985. The Mer Bleue Spotted Turtles: results of 1984 study. Conservation Studies Publication Number 37, National Capital Commission, Ottawa, Ontario. 7 pages.

Oldham, M. J. 1991. Status report on the Spotted Turtle, *Clemmys guttata*, in Canada. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, Ontario.

Rexstad, E., and **K. Burnham**. 1992. User's Guide for Interactive Program CAPTURE – Abundance estimation of closed animal populations. Self-published document.

Literature Cited

Brooks, R. J., M. A. Krawchuk, C. Stevens, and **N. Koper**. 1997. Testing the precision and accuracy of age estimation using lines in scutes of *Chelydra serpentina* and *Chrysemys picta*. Journal of Herpetology 31: 521-529.

Cagle, F. R. 1939. A system of marking turtles for future identification. Copeia 1939: 170-173.

Chippindale, P. 1989. Courtship and nesting records for Spotted Turtles, *Clemmys guttata* in Mer Bleue Bog, southeastern Ontario. Canadian Field-Naturalist 103: 289-291.

Cook, F. R., J. D. LaFontaine, S. Black, L. Luciuk, and **R. V. Lindsay**. 1980. Spotted Turtles (*Clemmys guttata*) in eastern Ontario and adjacent Quebec. The Canadian Field-Naturalist 94: 441-415.

Ernst, C. H., J. E. Lovich, and **R. W. Barbour**. 1994. Turtles of the United States and Canada. Smithsonian Institution, Washington D.C.

Gibbs, J. P., and **G. D. Amato**. 2000. Genetics and demography in turtle conservation. Pages 207-217 *in* Turtle Conservation. *Edited by* M. W. Klemens. Smithsonian Institution Press, Washington, D.C.

Haxton, T. J. 1998. Home range and habitat selectivity of Spotted Turtles (*Clemmys guttata*) in central Ontario: Implications for a management strategy. Master's thesis, Trent University, Peterborough, Ontario

Haxton, T., and **M. Berrill**. 1999. Habitat selectivity of *Clemmys guttata* in central Ontario. Canadian Journal of Zoology 77: 593-599.

Hilton-Taylor, C. 2000. 2000 IUCN Red List of Threatened Species. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland and Cambridge, UK.

Lewis, T. L., and **J. Ritzenhaler**. 1997. Characteristics of hibernacula use by spotted turtles, *Clemmys guttata*, in Ohio. Chelonian Conservation and Biology 2: 611-615.

Litzgus, J. D., and **R. J. Brooks**. 1998a. Growth in a cold environment: body size and sexual maturity in a northern population of spotted turtles, *Clemmys guttata*. Canadian Journal of Zoology 76: 773-782.

Litzgus, J. D., and **R. J. Brooks**. 1998b. Testing the validity of counts of plastral scute rings in spotted turtles, *Clemmys guttata*. Copeia 1998: 222-225.

Litzgus, J. D., J. P. Costanzo, R. J. Brooks, and **R. E. Lee, Jr.** 1999. Phenology and ecology of hibernation in spotted turtles (*Clemmys guttata*) near the northern limit of their range. Canadian Journal of Zoology 77: 1348-1357.

Milam, J. C., and **S. M. Melvin**. 2001. Density, habitat use, movements, and conservation of spotted turtles (*Clemmys guttata*) in Massachusetts. Journal of Herpetology 35: 418-427.

Ryan, B. F., and **B. L. Joiner**. 1994. Minitab Handbook. Third edition. Duxbury Press, Belmont California.

Seburn, D., and **C. Seburn**. 2000. Conservation Priorities for the Amphibians and Reptiles of Canada. World Wildlife Fund Canada and Canadian Amphibian and Reptile Conservation Network.

Received 10 February 2002
Accepted 10 February 2004

First record of the European Giant File Clam, *Acesta excavata* (Bivalvia: Pectinoidea: Limidae), in the Northwest Atlantic

JEAN-MARC GAGNON[1] and RICHARD L. HAEDRICH[2]

[1] Collections Division, Canadian Museum of Nature, P.O. Box 3443, Station "D", Ottawa K1P 6P4 Canada
[2] Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X7 Canada

Gagnon, Jean-Marc, and Richard L. Haedrich. 2003. First record of the European Giant File Clam, *Acesta excavata* (Bivalvia: Pectinoidea: Limidae), in the Northwest Atlantic. Canadian Field-Naturalists 117(3): 440–447.

Two large bivalve specimens collected in Bay d'Espoir, a deep fjord situated on the south coast of Newfoundland, are described and identified as belonging to the species *Acesta excavata* (Fabricius 1779). *In situ* observations onboard the manned submersible *PISCES IV* and color videos have provided information on the vertical distribution, density and habitat of the species. Maximum abundances of about 15 large individuals/m^2 occurred on sheltered rock outcrops at depth ranging from 550 to 775 m, where warm (6°C) continental slope water is found. Differences in shape and thickness between the valves of the two specimens appear to be related to the degree of exposure to rock falls (i.e., sheltered versus exposed habitat). Prior to this account, the European Giant File Clam had never been encountered west of the Azores Islands in the North Atlantic.

Key Words: *Acesta excavata*, European Giant File Clam, Limidae, Northwest Atlantic, fjord, Newfoundland.

Since the original description of the European Giant File Clam, *Acesta excavata,* by Fabricius (=*Ostrea excavata*; 1779), records for this species have shown a geographic range extending over most of the Northeast Atlantic, from the Norwegian and Greenland Seas to the Senegal coast (including the Azores and Canary Islands), and into the Mediterannean Sea (Barsotti 1975; Ghisotti 1979; Rocchini 1983; Carcassi 1983). Recorded depths vary between 90 m and 3200 m, although most occurrences reported since 1969 have been from the 200-800 m depth range (Ghisotti 1979). In the Krosfjord (Norway), the species is frequently encountered on rocky substrates between 100 and 400 m (Gilmour 1990). In many instances, *A. excavata* was found in association with the white deep-water coral *Madrepora oculata* (Rocchini 1983; Carcassi 1983). In the entire Atlantic Basin, only three other living species of Giant File Clams have been recorded: *A. bullisi* H. E. Vokes, 1963 from the Gulf of Mexico, *A. columbiana* H. E. Vokes, 1970 from the Caribbean Sea and *A. angolensis* Adam and Knudsen, 1955 from off the coast of Angola (Vokes 1963a, 1963b, 1970). To date, *Acesta excavata* is the only giant file clam species to have been observed in the Northwest Atlantic (Haedrich and Gagnon 1991) .

During a benthic study initiated in 1984 in Bay d'Espoir, a deep fjord situated along the south coast of Newfoundland, Canada, one large, sub-fossilized valve was recovered from sub-surface sediments by a grab, along with fragments of smaller but similar shells. These were tentatively identified to the genus *Acesta*. Although side-echoing of the depth sounder in this deep narrow fjord precluded reliable depth records, at least 740 m of wire had been released for the sample. Bottom-triggered photographs from the same area revealed no such shells on the sediment surface.

In 1985, the availability of a manned submersible allowed a closer examination of an important portion of the benthos on slopes that could not be sampled by conventional methods. Results of two submersible dives down to almost 800 m have yielded a wealth of information on the fauna in the form of direct in-situ observations, colour videos and still photographs. In addition, one complete live specimen of Giant File Clam (Limidae) was recovered from the rock wall, using the hydraulic arm of the submersible.

This paper describes the specimens collected (valves and soft parts) and confirms their identity as *Acesta excavata* (Fabricius 1779), based on diagnostic characters of the valves: shape, size and external ornamentation, shape of the ligamental pit and development of the auricles. These specimens are deposited in the Mollusc Collection of the Canadian Museum of Nature, in Ottawa. We also report information on the density and distribution of that species in Bay d'Espoir in relation to substratum type, water temperature, salinity as well as depth. An overall description of the fauna and habitat based on observations obtained during the submersible dives is presented elsewhere (Haedrich and Gagnon 1991).

Description of the Environment

Bay d'Espoir is a fjord situated along the south coast of Newfoundland (Figure 1; 47° 40' N, 56° 08' W). In the eastern portion of its outer basin (near Goblin Head), where specimens of *Acesta* were found, maximum depth reaches 794 m. There, at least 30% of the bottom consists of rock walls with slopes greater than

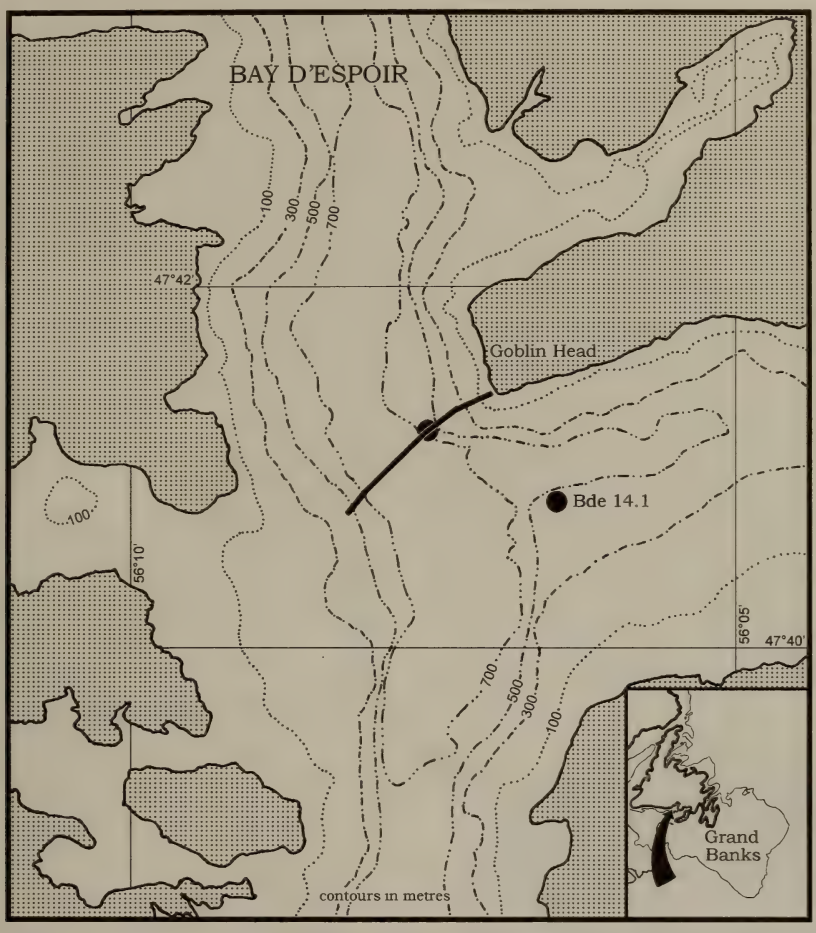


FIGURE 1. Collection sites of the Giant File Clam, *Acesta excavata,* (filled circles) in Bay d'Espoir, Newfoundland.

40 degrees and there are frequent overhangs (Figure 2). In areas where slopes are not as steep, the bottom is mostly made up of silty sediments. Benthic biomass in this basin appears to be important and primarily dominated by suspension and filter feeders such as sponges, several species of anemones, sea pens, the stalked cirriped *Arcoscalpellum mitchellotianum*, and Giant File Clam (*Acesta*). This rich invertebrate fauna is supported by a high zooplanktonic biomass (Haedrich and Gagnon 1991), although no estimates of surface primary production are available for this area.

The water column in the outer basin is divided in four distinct layers on the basis of temperature and salinity (Haedrich and Gagnon 1991; Figure 2). Below 250 m, which corresponds approximately to the sill depth at the entrance of the fjord, benthic communities are exposed to a uniformly warm (5.0 to 6.5°C), saline (34.6‰) and stable water mass derived from the continental slope water. Above, a cold water layer (40-160 m, -1.0 to 1.0°C) associated with the less saline Labrador Current and a transition layer (160-220 m, 1.0 to 5.0°C) maintain the deep isolated layer; only limited exchanges occur with the Laurentian Modified Slope Water from the outside (Hay and deYoung 1983; Richard and Haedrich 1987).

Materials and Methods

The first specimens of *Acesta* were collected during a benthic sampling program conducted in the outer deep basin of Bay d'Espoir, Newfoundland, Canada, on 10 December 1984. During that sampling, one large, complete valve and fragments of smaller valves were found in the anoxic, muddy sub-surface sediment of a 0.1m^2 van Veen grab sample from a site to the southeast of Goblin Head, at approximately 600-700 m depth (Figure 1; circa station BdE14.1, 47°40.8' N, 56°06.5' W). On 26 June 1985, during a dive onboard the manned submersible *PISCES IV*, a complete, living specimen was retrieved with the hydraulic arm from the rock wall at the foot of Goblin Head (47°41.2' N, 56°07.6' W), at 750 m depth (Figures 1 and 2). Information on the density and vertical

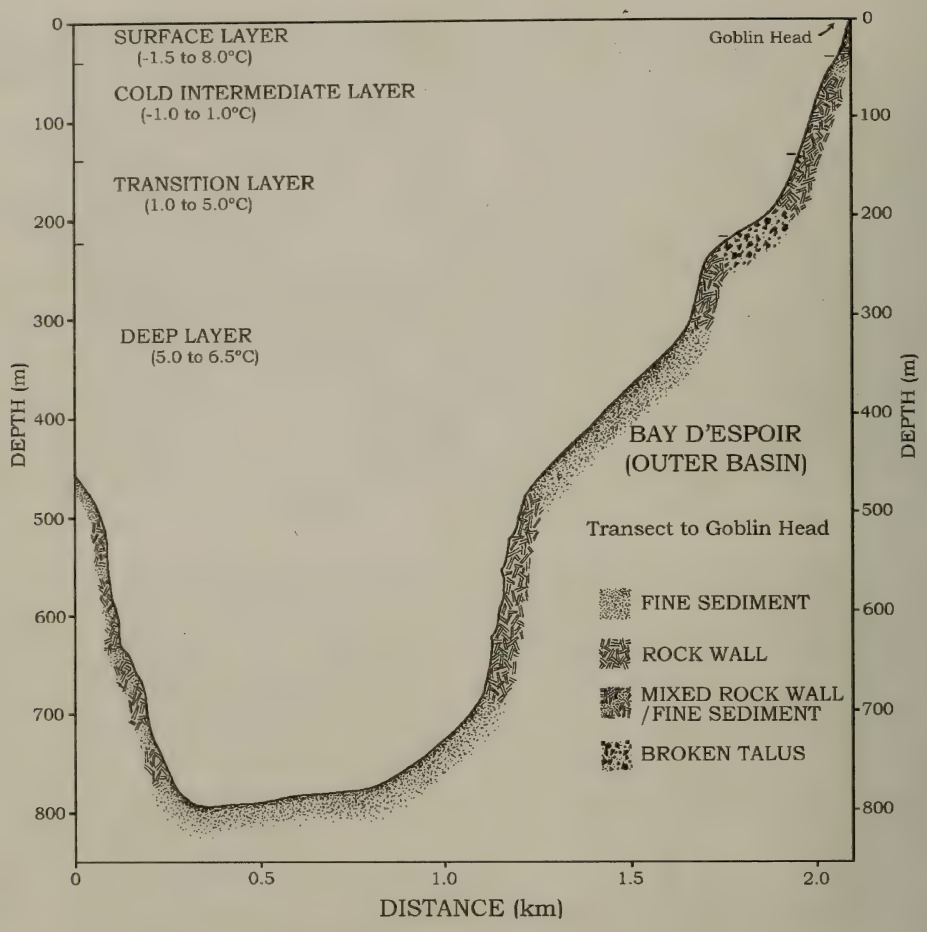


FIGURE 2. Cross-section of the outer basin along the submersible dive transect.

distribution of the species was also recorded during the dive of June 26 and 27 through direct in-situ observations, color videos using an external camera, and color photographs using an external Photosea camera and a hand-held camera through the port-hole.

Results and Discussion

Description of specimens

The first specimen of *Acesta excavata* (catalogue number CMNML 092957), which was collected with a bottom grab near Station BdE14.1, consisted of a complete right valve (height 112.5 mm, width 81 mm; Figures 3-5). The shell is relatively thin (0.93 mm), dark grey on the outside and white on the inside (Figures 3 and 4). Deterioration of the inner layer is evident as much of the luster on the nacre layer has disappeared. The external ornamentation of the valve, however, appears intact and is composed of weak, somewhat irregular radial ribs which are more developed in the anterior and posterior region of the valve. In the median portion of the shell surface, these ribs resemble more shallowly impressed, irregular grooves (Figure 3). As described by Vokes (1963a) for *Acesta excavata*, the straightness of the ribs is mostly affected by the presence of pronounced growth rings. The anterior auricle is highly reduced through the encroachment of the large excavate lunule. The ligamental pit is strongly oblique (Figure 5).

There is a striking resemblance between this specimen from Bay d'Espoir (Figure 3) and those illustrated by Barsotti (1975), Ghisotti (1979) and Rocchini (1983). In fact, shell characteristics for this specimen correspond well to those of specimens of *Acesta excavata* examined from the Northeast Atlantic (including the Azores Islands), the Norwegian Sea, the Mediterranean Sea (Table 1). Its shell height/width ratio (1.39) falls within the variation of that observed in these European specimens (mean= 1.34, standard deviation= 0.049, n=27).

The second specimen (catalogue number CMNML 092958; Figures 6-8) was a complete, living individual, only slightly damaged during its recovery by the hydraulic arm of the submersible. The damage was mainly due to the force necessary to break the byssal

attachment to the rock wall. The left valve, however, shows signs of shell damage sustained by the animal earlier in its life (Figure 6). This past injury apparently resulted in abnormal growth of the animal. While the shell height (112.0 mm) is very similar to that of our first specimen, it is significantly wider (94.5 mm), with a height/width ratio of 1.19. The animal was originally injured in the posterior region of the shell (see Figure 6, shell margin at height 34 mm), causing a greater growth in that region of the shell relative to the rest and resulting in the wider, less elongated appearance of the specimen. The pathological condition of this specimen is also reflected by the distorted margin of the lunule (Figures 7-9). Valves are also thicker (1.1 mm) than that of the first specimen, and mostly white. Otherwise, the ornamentation of the shell, the shape of the ligamental pit and muscle scars are comparable to those of the first specimen. The differences observed between the two specimens may be the result of living in a sheltered vs. exposed habitat. As discussed in the following section, animals living under overhangs are protected from rock falls.

Very little information is available in the literature on the soft parts of *Acesta excavata*, hard parts being typically used to identify bivalves. Figures 9-11 show some important characteristics such as the long pallial tentacles along the mantle margin (typical of all Limoida; Gilmour 1990), eight strong byssal treads and the deeply grooved foot. When freshly collected, margins of the mantle and its tentacles were bright orange, the remaining soft parts being mostly pale orange. Gilmour (1990) examined the significance of foot reversal in Limoida and described the arrangement of muscles on freshly collected *Acesta excavata* specimens from the Krosfjord in Norway. The overall pattern of muscle disposition on our specimen corresponds well with that described by Gilmour. The slight difference in the position of the anterior pedal retractor and the not readily visible anterior byssal retractor are not believed to be significant (T. H. J. Gilmour, personal communication).

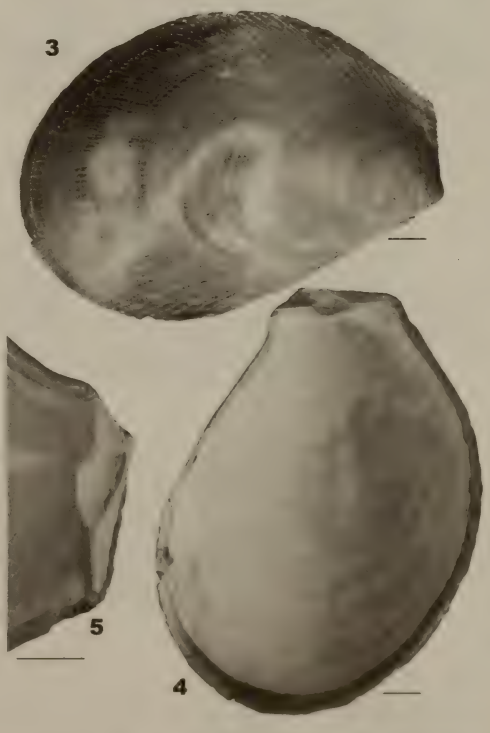
In situ observations

To our knowledge, this is the first *in situ* observation of the European Giant File Clam, *Acesta excavata*. The species was encountered on rock walls and outcrops only in the deepest part of the outer basin, between approximately 550 and 775 m. Water temperature within that depth range was 6.3±0.1°C. Because rock faces are infrequent between 500 and 300 m (Figure 2), it is not possible to establish an accurate upper limit to the bathymetric distribution of *A. excavata* in Bay d'Espoir.

In areas where the rocky substrate is exposed to sedimentation, and potentially to rock falls (Figure 12), total animal biomass appears much lower than in sheltered areas (Figure 13). The Giant File Clam shared these habitats primarily with anemones and sponges; colonial anemones were particularly dominant under overhangs (Figure 13). We found no indication of the presence of the white coral *Madrepora oculata* which is frequently found in association with *Acesta excavata* in the Northeast Atlantic (Fosså and Mortensen 1998) and the Mediterranean (Parenzan 1974; Ghisotti 1979; Rocchini 1983; Carcassi 1983). Estimates of density are difficult to obtain due to the patchy distribution of *Acesta* on the rocky substrate and the lack of a reference scale when surveying with the submersible. When present, however, densities appear to vary from few to 10-15 individuals per metre^2; this is probably a conservative estimate since only the large individuals that could be distinguished from the orange anemone *Actinauge* sp. were counted.

Origin of the Northwest Atlantic population

The discovery of *Acesta excavata* off southern Newfoundland represents a significant extension to its previously known geographic range by probably more than 2100 km. This Newfoundland population of *A. excavata* may be a relict from a previously wider distribution, although many deepwater species found in Bay d'Espoir are typically found on the Eastern Canadian continental slope and the St. Lawrence Channel. Alternatively, *A. excavata* may have a more continuous distribution in the Northwest Atlantic at

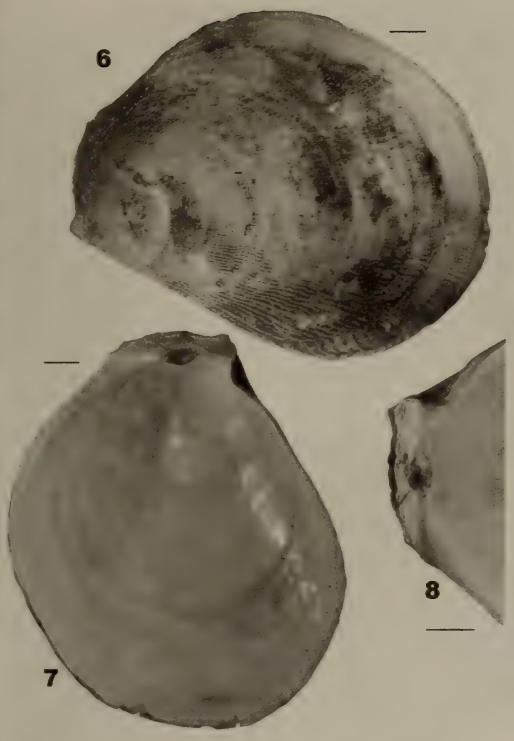


FIGURES 3-5. *Acesta excavata* specimen #1 (catalogue number CMNML 092957), right valve; height: 11.25 cm, width: 8.0 cm. 3. Exterior view. 4. Interior view. 5. Hinge view.

TABLE 1. Variability of height/width ratio in *Acesta excavata* over its extended geographic range, based on specimens examined in collections and values reported in the literature.

Geographic region	Source / institution *	Specimen catalogue no.	Specimen description	Shell dimensions (mm) height	Shell dimensions (mm) width	H/W ratio
Newfoundland	CMN	CMNML 092957	1 valve	112.5	81.0	1.39
	CMN	CMNML 092958	whole	112.0	94.5	1.19
Azores Islands	CMN	CMNML 042946	1 valve	93.5	67.0	1.40
	CMN	CMNML 042947	1 valve	98.0	73.5	1.33
Northeast Atlantic /	CMN	CMNML 009259	whole	97.0	71.0	1.37
Norweglan Sea	BMNH	not available	whole	97.5	70.5	1.38
	BMNH	not available	whole	61.0	48.0	1.27
	BMNH	not available	whole	69.0	51.0	1.35
	FMNH	160769	1 valve	108.3	82.2	1.32
	FMNH	2404	2 valves	120.9	88.0	1.37
	MNHN	not available	whole	163.0	117.0	1.39
	UC/MOL	not available	2 valves	94.5	71.0	1.33
	UC/MOL	not available	2 valves	138.0	107.0	1.29
	UC/MOL	not available	1 valve	135.0	105.0	1.29
	UC/MOL	not available	1 valve	215.0	160.0	1.34
	UC/MOL	not available	1 valve	10.0	8.0	1.25
	UC/MOL	1223	2 valves	109.0	81.5	1.34
	UMM	not available	1 valve	161.0	119.0	1.35
	McAndrew 1857	not available	from Vokes 1963a	140.0	108.0	1.30
	Lamy 1930	not available	from Vokes 1963a	170.0	125.0	1.36
	Philippi 1900	not available	drawing	135.0	105.0	1.29
	Thiele 1918-20	not available	text	150.0	105.0	1.43
	Abbott and Dance 1982	not available	photograph	100.0	75.0	1.33
Mediterranean Sea	FMNH	2401	2 valves	135.6	103.1	1.32
	Parenzan 1974	not available	text description	140.0	103.0	1.36
	Barsotti 1975	not available	subfossil, text & photograph	140.0	103.0	1.38
	Ghisotti 1979	not available	text description	56.5	42.3	1.34
	Carcassi 1983	not available	text description	50.0	35.0	1.43
	Carcassi 1983	not available	text description	50.0	35.0	1.43
	Carcassi 1983	not available	text description	65.0	50.0	1.30
	Rocchini 1983	not available	text description	63.0	45.0	1.40

* CMN: Canadian Museum of Nature, Ottawa, Canada; BNHM: The (British) Natural History Museum, London, England; MNHN: Muséum national d'histoire naturelle, Paris, France; UMM: University of Manchester Museum, Manchester, England; UC/MOL: University of Cambridge/Mollusc Collection, Cambridge, England; FMNH: The Field Museum of Natural History, Chicago, U.S.A.



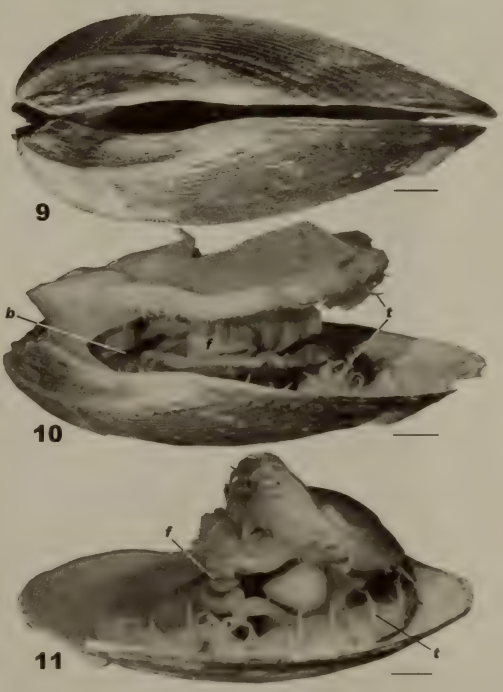
FIGURES 6-8. *Acesta excavata* specimen #2 (catalogue number CMNML 092958), left valve; height: 11.2 cm, width: 9.45 cm. 6. Exterior view. 7. Interior view. 8. Hinge view of left valve.

present but has only been recovered from Bay d'Espoir.

There have been relatively few surveys of bathyal communities in the Northwest Atlantic (Grassle et al. 1975; Haedrich et al. 1980), and particularly on deep-water hard substrata along the eastern Canadian and Greenland continental slopes (Houston and Haedrich 1984). The few surveys that have been undertaken along the eastern Canadian and United States slopes, including photographic explorations of the wreck of the RMS *TITANIC* (P. Pocklington, personal communication), did not reveal the presence of *A. excavata*. Further sampling surveys are necessary in areas of the Northwest Atlantic where suitable *A. excavata* habitats (e.g., deep-basin bays, continental slope and bathyal rocky outcrops) exist to determine the full extent of its distribution. Also needed is information on the larval stages of *A. excavata* and their dispersal in the water column, to establish whether they occur in prominent ocean current systems between the Northeast and Northwest Atlantic and could account for the establishment of the European Giant File Clam in Bay d'Espoir, Newfoundland.

Acknowledgments

We thank the other scientific members of the dive team — Jack Foley, Roy Ficken, Bob Hooper and David Schneider — for their help and participation in the field program onboard the *Pandora/PISCES IV*. This work would not have been possible without the logistic support of the captains and crews of the C.S.S. *DAWSON* and *Pandora/PISCES IV;* ships and submersible were made available to us by the Department of Fisheries and Oceans Canada (DFO). We further extend our gratitude to Roy Ficken for providing us with his expertise as photographer during the dives and subsequently, when producing figures for this publication. We also thank Harold E. Vokes and Thomas Gilmour for their help in confirming the identification of the specimens; Rudolph Scheltema, Bernard Sainte-Marie, David Barr, André Martel and four anonymous reviewers for their comments on the manuscript, and Leisha Clarke-Doherty and Mélanie Gaudet for editorial assistance. This work was funded in part by a grant from the Natural Sciences and Engineering Research Council (NSERC) to R. L. H. and a DFO/NSERC post-doctoral fellowship to J.-M. G.



FIGURES 9-11. *Acesta excavata* specimen #2 (catalogue number CMNML 092958). 9. Anterior view of complete animal. 10 and 11. Anterior and ventro-posterior views of animal in right valve, showing byssus (*b*), grooved foot (*f*), and pallial tentacles (*t*).

FIGURES 12-13. Living *Acesta excavata* on the rock walls of Bay d'Espoir. 12. Sheltered under overhang, circa 650 m. 13. Exposed, circa 550 m.

Literature Cited

Abbott, R. T., and **S. P. Dance.** 1982. A compendium of seashells. E. P. Dutton, New York, New York.

Barsotti, G. 1975. Superfamilia Pectinacea Rafinesque, 1815, Fam. Limidae. La Conchiglia, Roma, 7 (71-72): 3-6.

Carcassi, A. 1983. Uteriore ritrovamento di *Acesta excavata* vivente in Mediterraneo. Bollettino Malacologico 19: 264.

Fabricius, J. C. 1779. Reise nach Norwegen: Hamburg. I-LXIII, 388 pages.

Fosså, J. H., and **P. B. Mortensen**. 1998. Artsmangfoldet på *Lophelia*-korallrev og metoder for kartlegging og overvåkning. Havforskningsinstituttet (Burgen), Fisken og Havet NR. 17, 95 pages.

Ghisotti, F. 1979. Ritrovamento di *Acesta* (*Acesta*) *excavata* (Fabricius, 1779) vivente in Mediterraneo. Bollettino Malacologico 15: 57-66.

Gilmour, T. H. J. 1990. The adaptative significance of foot reversal in the Limoida. Pages 249-263 *in* The Bivalvia - Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge. *Edited by* B. Morton. Hong Kong University Press, Hong Kong.

Grassle, J. F., H. L. Sanders, G. T. Rowe, and **T. McLennan**. 1975. Patterns and zonation: a study of the bathyal megafauna using the research submersible *Alvin*. Deep-Sea Research 22: 457-481.

Haedrich, R. L., and **J.-M. Gagnon**. 1991. Rock wall fauna in a deep Newfoundland fiord. Continental Shelf Research 11: 1199-1207.

Haedrich, R. L., G. T. Rowe, and **P. T. Polloni**. 1980. The megafauna in the deep sea south of New England, U.S.A. Marine Biology 57: 165-179.

Hay, A. E., and **B. deYoung**. 1983. An oceanographic flip-flop: deep water exchange in Fortune Bay, Newfoundland. Journal of Geophysical Research 94: 843-853.

Houston, K., and **R. L. Haedrich**. 1984. Abundance and biomass of macrobenthos in the vicinity of Carson submarine canyon, northwest Atlantic ocean. Marine Biology 82: 301-305.

Lamy, E. 1930-31. Révision des Limidæ vivants du Muséum National d'Histoire Naturelle de Paris. Journal de Conchyliologie 74: 89-269.

McAndrew, R. 1857. Report on marine testaceous Mollusca of the Northeast Atlantic and neighboring seas, and physical conditions affecting development. Pages 101-144 *in* Report of the British Association for the Advancement of Sciences.

Parenzan, P. 1974. Carta d'identità delle conchiglie del Mediterraneo. Volume II Bivalvi, prima parte. Bios Taras Publishing, Taranto, Italy. Pages 122-123, plate 26.

Philippi, E. 1900. Beiträge zur Morphologie and Phylogenie der Lamellibranchier. III. *Lima* und ihre Untergattungen, Zeitschift der Deutsche Geologische Gesellschaft 52: 619-639, Plate 24.

Richard, J. M., and **R. L. Haedrich**. 1987. The mesopelagic fish faunas of two fjords differing in physical oceanography. Pages 193-200 *in* Proceedings of the 5th Congress of European Ichthyologists. *Edited by* S. O. Kullander. Stockholm.

Rocchini, R. 1983. *Acesta excavata* (Fabricius, 1779), nuovo ritrovamento in Mediterraneo. Bollettino Malacologico 19: 83-86.

Thiele, J. 1918-20. Familia Limidæ. Conchulien-Cabinet. Verlag von Bauer & Raspe, Nürnburg, Germany. 66 pages. 10 plates.

Vokes, H. E. 1963a. Studies on tertiary and recent giant Limidæ. Tulane Studies in Geology 1: 73-92.

Vokes, H. E. 1963b. Additions to a catalogue of the described recent and tertiary species of *Acesta* and *Plicacesta*. Tulane Studies in Geology 2: 18-20.

Vokes, H. E. 1970. Two new species of deepwater bivalves from the Caribbean Sea. The Veliger 12: 357-361.

Received 10 September 2002
Accepted 6 January 2004

Additions and Range Extensions to the Vascular Plant Flora of the Continental Northwest Territories and Nunavut, Canada, II

WILLIAM J. CODY[1], KENNETH L. READING[2], and JENNIFER M. LINE[3,4]

[1]Biological Resources Program, Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, Central Experimental Farm, Ottawa, Ontario K1A 0C6 Canada
[2] 11 Colborne St., Thornhill, Ontario L3T 1Z4 Canada
[3] Botany Department, University of Manitoba, Winnipeg, Manitoba R3T 2N2 Canada
[4] 7178 7th Avenue, Whitehorse, Yukon Territory Y1A 1R1 Canada

Cody, William J., Kenneth L. Reading, and Jennifer M. Line. 2003. Additions and range extensions to the vascular plant flora of the continental Northwest Territories, Canada, II. Canadian Field-Naturalist 117(3): 448-465.

Based on field reconnaissance since the publication of *Flora of the Continental Northwest Territories* in 1980, particularly in the District of Keewatin and northeastern District of Mackenzie (Nunavut) and Nahanni National Park, information is provided on geographically significant plant occurrences. One new taxon, *Polemonium boreale* forma *albiflorum,* is described, fourteen native taxa are reported as new to the region: *Carex hoodii*, *C. microptera*, *C. petasata*, *Corispermum hookeri*, *C. ochotense*, *Danthonia spicata*, *Draba stenoloba*, *Erysisnum coarctatum*, *Halenia deflexa*, *Polygonum fowleri*, *P. ramosissimum*, *Salix rotundifolia* ssp. *rotundifolia, Silene uralensis* ssp. *ogilviensis*, and *Vaccinium ovalifolium.* Five introduced taxa, *Crepis tectorum*, *Corispermum villosum*, *Deschampsia elongata*, *D. incisa* var. *incisa,* and *Medicago sativa* ssp. *falcata* are new to the flora of the region. Two native taxa, *Danthonia intermedia* and *Potentilla porsildiorum* are deleted from the flora and *Ranunculus aquatilis* var *hispidulus* is placed in synonymy. Significant range extensions for 125 native and one introduced taxon are included.

Key Words: Vascular plants, Mackenzie, Keewatin, flora, new records, range extensions, phytogeography.

Since the publication of *Vascular Plants of Continental Northwest Territories, Canada* (Porsild and Cody 1980) continued field and taxonomic studies have revealed the presence of additional taxa in the Territories that were unknown to the authors at the time of publication. These include both introduced taxa (Cody et al. 2000, 2003; Wein et al. 1992); native taxa in the far north (Cody et al. 1984, 1989, 1992); various areas (Cody 1996, 1998, Cody and Johnston 2003; and Timoney 2001). In addition, McJannet et al. (1995) have produced a monograph entitled *Rare Vascular Plants in the Northwest Territories*. The present paper serves to further update our knowledge of the floristic information which is essential for biological research and ongoing work relating to agriculture, forestry, sustainable resource management and wildlife management.

In this paper the authors have continued to use the historic names "District of Keewatin" and "District of Mackenzie" to follow the format of Porsild and Cody (1980) *Vascular Plants of Continental Northwest Territories, Canada* and subsequent publications. However, continental "Keewatin" and the former northeastern portion of the District of Mackenzie are now part of the recently defined Continental Nunavut Territory.

A synopsis of the taxa addressed in the body of this paper follows with species listed in alphabetical order within categories. The taxa are then discussed in an annotated list by family in the same taxonomic order as presented in the *Flora of the Continental Northwest Territories* together with citation of specimens and other pertinent information.

Synoptic list by Continental Northwest Territories Status

New Taxon to the Continental Northwest Territories (1):

Polemonium boreale forma *albiflorum*

Native Taxa new to the Continental Northwest Territories (14):

Carex hoodii
Carex microptera
Carex petasata
Corispermum hookeri
Corispermum ochotense
Danthonia spicata
Draba stenoloba
Erysimum coarctatum
Halenia deflexa
Polygonum fowleri
Polygonum ramosissimum
Salix rotundifolia ssp. *rotundifolia*
Silene uralensis ssp. *ogilviensis*
Vaccinium ovalifolium

Introduced Taxa New to the Continental Northwest Territories (5):

Crepis tectorum
Corispermum villosum
Deschampsia elongata
Descurainia incisa var. *incisa*
Medicago sativa ssp. *falcata*

Range extensions of native taxa in the Continental Northwest Territories (125):

Adoxa moschatellina
Agrostis mertensii ssp. *mertensii*
Alnus crispa

Angelica lucida
Apocynum cannabinum var. *glaberrimum*
Arctagrostis latifolia
Artemisia campestris
Artemisia tilesii
Aster sibiricus
Aster spathulatus
Astragalus australis
Botrychium lunaria
Caltha natans
Caltha palustris ssp. *arctica*
Carex arcta
Carex disperma
Carex maritima
Carex tenuiflora
Chamaedaphne calyculata
Chrysanthemum integrifolium
Chrysosplenium tetrandrum
Corallorhiza trifida
Crassula aquatica
Cystopteris fragilis
Cystopteris montana
Draba alpina
Draba cinerea
Draba glabella
Draba lactea
Eleocharis acicularis
Eleocharis quinqueflora
Elymus canadensis
Epilobium anagalidifolium
Epilobium arcticum
Epilobium davuricum
Epilobium hornemannii
Epilobium leptophyllum
Epilobium palustre
Equisetum arvense
Equisetum palustre
Equisetum scirpoides
Equisetum variegatum
Eriophorum viridi-carinatum
Gentianella propinqua ssp. *propinqua*
Gymnocarpium dryopteris ssp. *dryopteris*
Juncus balticus ssp. *alaskanus*
Juncus filiformis
Juniperus communis
Kobresia myosuroides
Kobresia siberica
Koenigia islandica
Ledum groenlandicum
Linnaea borealis var. *americana*
Lobelia dortmanna
Lomatogonium rotatum ssp. *rotatum*
Lycopodium clavatum var. *monostachyon*
Lycopodium complanatum
Lycopus uniflorus
Maianthemum trifolium
Menyanthes trifoliata
Mertensia drummondii
Minuartia rossii
Minuartia rubella
Osmorhiza depauperata
Oxycoccus microcarpus
Oxytropis arctica
Oxytropis deflexa ssp. *foliolosa*
Papaver macounii ssp. *discolor*
Parnassia kotzebuei
Parnassia palustris var. *neogaea*
Pedicularis flammea
Pedicularis lanata
Pedicularis macrodonta
Petasites frigidus ssp. *palmatus*
Petasites sagitatus
Phalaris arundinacea
Phyllodoce coerulea
Phyllodoce empetriformis
Platanthera aquilonis
Platanthera obtusata
Poa arctica
Polemonium boreale
Polygonum hudsonianum
Potamogeton natans
Potamogeton obtusifolius
Potamogeton richardsonii
Potamogeton vaginatus
Potentilla hyparctica
Potentilla nivea
Potentilla tridentata
Primula incana
Pyrola minor
Ranunculus flammula
Ranunculus flammula var. *filiformis*
Ranunculus nivalis
Ranunculus pallasii
Ranunculus pygmaeus
Ranunculus sulphureus
Rubus arcticus ssp. *acaulis*
Salix athabascensis
Salix lutea
Salix polaris
Saxifraga caespitosa ssp. *uniflora*
Saxifraga cernua
Saxifraga foliolosa
Saxifraga hieracifolia
Saxifraga hirculus
Saxifraga nelsoniana ssp. *porsildiana*
Saxifraga nivalis
Scirpus validus
Shepherdia canadensis
Silene taimyrensis
Spiraea beauverdiana
Stellaria borealis
Stellaria crassifolia
Suaeda calceoliformis
Subularia aquatica ssp. *americana*
Taraxacum lyratum
Vahlodea atropurpurea ssp. *latifolia*
Viola adunca
Viola epipsila ssp. *repens*
Viola renifolia var. *brainerdii*
Woodsia alpina
Woodsia glabella
Woodsia ilvensis

Deletions of native taxa from the Continental Northwest Territories (2):

Danthonia intermedia
Potentilla porsildiorum

Range extension of introduced taxon in the Continental Northwest Territories (1):
Melilotus alba

Comments on native taxa in the Continental Northwest Territories (2):
Gymnocarpium jessoense ssp. *parvulum*
Ranunculus aquatilis var. *hispidulus*

Annotated List by Family

LYCOPODIACEAE

Lycopodium clavatum L. var. *monostachyon* Hook. and Grev., Common Club-moss – MACKENZIE: open *Pinus banksiana/Picea mariana/Alnus crispa/Shepherdia canadensis*, Fort Liard region, 60°29'N 123°25'W, *R. Mueller FTL-18-82*, 14 Aug. 1994 (DAO); KEEWATIN: Long Lake SE of Bissett Lake, 63°49'N 95°15'W, *K.L. Reading s.n.*, 28 July 1982 (DAO); west of Griffin Lake, 61°19'00"N 98°51'00"W, *K.L. Reading s.n.*, 12 July 1992 (DAO).

The first specimen cited above is an extension of the known range in the Northwest Territories south from the Yohin Ridge in Nahanni National Park of about 125 kilometers (Cody and Britton 1989). It was also recently reported from Beavercrow Ridge in extreme southeast Yukon Territory (Cody et al. 2001). The second specimen cited above is an extension of the known range in the District of Keewatin of about 340 kilometers northeast of the only site in that District known to Porsild and Cody (1980); the third specimen is from the same region as that mapped by Porsild and Cody (1980).

Lycopodium complanatum L., Flatbranch Club-moss – KEEWATIN: Griffin Lake, 61°19'00"N 98°51'00"W, *K.L. Reading s.n.*, 15 July 1992 (DAO); south of east arm of Tyrell Arm of Yathkyed Lake, 62°20'50"N 97°33'40"W, *K.L. Reading s.n.*, 26 July 1985 (DAO).

Porsild and Cody (1980) knew this species in Continental District of Keewatin from only two localities in the southwest. The second specimen cited above is the northernmost yet found in Keewatin.

EQUISETACEAE

Equisetum arvense L., Field Horsetail – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'W, *K.L. Reading 27*, 10 Oct. 1998 (DAO).

The specimen cited above is from a site about 120 kilometers south of the vicinity of Coppermine and 80 kilometers east of the east end of Great Bear Lake (Porsild and Cody 1980).

Equisetum palustre L., Marsh Horsetail – MACKENZIE: Tin Can Hill, south of Rat Lake, Yellowknife, 62°26'N 114°21'15"W, *K.L. Reading s.n.*, 1982 (DAO); Ski Club road, north of town of Yellowknife, 62°28'00"N 114°21'40"W, *K.L. Reading s.n.*, 1982 (DAO); KEEWATIN: south of Deep Bay on the Kazan River, 63°42'05"N 95°37'08"W, *K.L. Reading s.n.*, 3 Aug. 1982 (DAO); open fen-seeps, north of 30-mile Lake, 63°42'54"N 96°07'32"W, *K.L. Reading s.n.*, 21 July 1981 (DAO); south of Whale Lake, 63°45'55"N 96°04'10"W, *K.L. Reading s.n.*, 21 Aug. 1982 (DAO); Campsite peninsula, west shore of Bissett Lake, 63°46'38"N 95°26'12"W, *K.L. Reading s.n.*, 18 June 1982 (DAO).

The first two specimens cited above are an extension of the known range in the District of Mackenzie of about 200 kilometers north of sites south of Great Slave Lake. The remaining specimens from central District of mainland Keewatin are the first reported from that region.

Equisetum scirpoides Michx., Dwarf Scouring Rush – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'W, *K.L. Reading 28*, 15 Sept.–10 Oct. 1998 (DAO).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 120 kilometers northeast of a site adjacent to Port Radium at the east end of Great Bear Lake.

Equisetum variegatum Schleich., Variegated Horsetail – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'W, *K.L. Reading 29*, 10 Oct. 1998 (DAO).

The specimen cited above is from a site about 120 kilometers south of the vicinity of Coppermine (Porsild and Cody 1980).

OPHIOGLOSSACEAE

Botrychium lunaria (L.) Sw., Moonwort – MACKENZIE: rare, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 20-1*, 10 July 1999 (DAO); rare, same area, *K.L. Reading 37-1*, 6 Sept. 1999 (DAO); Coppermine River, *K.L. Reading s.n.*, 18 Sept. 1999 (DAO); KEEWATIN: north of Ducker Lake, 61°21'18"N 97°54'28"W, *K.L. Reading s.n.*, July 1990 (DAO).

In 1980 K. J. Hebden photographed a plant of this species at Bloody Falls, near the mouth of the Coppermine River (Cody 1996). The Mackenzie specimens cited above are from sites intermediate between Bloody Falls and the south shore of Great Bear Lake (Porsild and Cody 1980); the Keewatin specimen is the second known from that Territory 40 km ENE of Griffin Lake (Cody 1996).

ASPIDIACEAE

Cystopteris fragilis (L.) Bernh., Fragile Fern – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'W, *K.L. Reading 25*, 10 Oct. 1998 (DAO); KEEWATIN: cliffs south of Whale Lake, 63°46'58"N 96°02'37"W, *K.L. Reading s.n.*, 21 Aug. 1982 (DAO).

The first specimen cited above is from a site about 120 kilometers south of the vicinity of Coppermine and 80 kilometers east of the east end of Great Bear Lake (Porsild and Cody 1980). The second specimen is the fourth known record from the Continental District of Keewatin. It is a slight extension of the known range to the northeast.

Cystopteris montana (Lam.) Bernh., Mountain Bladder Fern – MACKENZIE: *Picea glauca-Abies lasiocarpa*, krummholz, Mackenzie Mountains, Liard Range, 60°36'N 123°47'W, *G. Brunner LR-10-5*, 12 Aug. 1994 (DAO).

This species was not included in the *Rare Plants in the Northwest Territories* (McJannet et al. 1995) because it has a widespread circumpolar range. The specimen cited above is an extension of the known range in the Territory of about 60 kilometers south from the vicinity of the junction of the South Nahanni and Liard rivers (Porsild and Cody 1980). It was, however, recently reported from the La Biche River area in southeastern Yukon Territory (Cody et al. 1998).

Gymnocarpium dryopteris (L.) Newm. ssp. *dryopteris* (*Dryopteris disjuncta* Am. auth.), Oak Fern – MACKENZIE: thicket, *Betula papyrifera/Alnus crispa, A. incana*, Fort Liard region, 60°09'N 123°42'W, *G. Brunner FTL-34-1*, 17 Aug. 1994 (DAO).

This species was considered rare in the Northwest Territories by Porsild and Cody (1980) because it was only known in the extreme south and in the Mackenzie Mountains region. It was not included in the *Rare Plants in the Northwest Territories* (McJannet et al. 1995) because it has a widespread circumpolar distribution. The specimen cited above is an extension of the known range in the Territory to the south from sites in the southern Mackenzie Mountains. It was also recently reported from the La Biche River and Mount Merrill regions in southeastern Yukon Territory (Cody et al. 1998).

Gymnocarpium jessoense (Koidz.) Koidz. ssp. *parvulum* Sarvela, Nahanni Oak-fern.

It has been brought to our attention that in the previous paper on additions and range extension of this region (Cody 1996) the longitude reported for this taxon should have been 98°40'W not 97°40'.

Woodsia alpina (Bolton) S.F. Gray, Northern Woodsia – KEEWATIN: East of Pebble Beach lake, 62°22'12"N 97°28'50"W, *K.L. Reading s.n.,* July 1985 (DAO).

The specimen cited above is only the third record for the Continental District of Keewatin and is a slight extension of the range mapped by Porsild and Cody (1980) to the south.

Woodsia glabella R.Br., Smooth Woodsia – KEEWATIN: east of Kazan River north of Big Bend, 63°46'58"N 95°36'00"W, *K.L. Reading s.n.,* 6 Aug. 1983 (DAO); in cave-like crevices of rocky escarpment face, south of Whale Lake, 68°46'58"N 96°02'37"W, *K.L. Reading s.n.*, 21 Aug. 1982 (DAO).

Porsild and Cody (1980) knew this taxon from only three localities in the Continental District of Keewatin, two in the central area and one adjacent to the Arctic Coast. The specimen cited above is an extension of the range in the central area to the east.

Woodsia ilvensis (L.) R.Br., Rusty Woodsia – KEEWATIN: east of Kazan River north of Big Bend, 63°46'58"N 95°36'00"W, *K.L. Reading s.n.,* 6 Aug. 1983 (DAO).

Porsild and Cody (1980) knew this species in the Continental District of Keewatin from two sites, one in the central area and one to the northeast south of the Arctic Circle. The specimen cited above is from a site east of the one in the central area.

PINACEAE

Juniperus communis L., Ground Juniper – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'W, *K.L. Reading 32*, 15 Sept.-10 Oct. 1998 (DAO).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 120 kilometers northeast of a site in the vicinity of Port Radium at the east end of Great Bear Lake.

POTAMOGETONACEAE

Potamogeton natans L. – MACKENZIE: small lake south of Cameron River road about 14 miles east of Yellowknife, 62°32'00"N 113°53'00"W, *K.L. Reading s.n.,* 17 Sept. 1995 (DAO); small lake south of Cameron River road about 22 miles east of Yellowknife, 62°31'44"N 113°51'30"W, *K.L. Reading s.n.,* 17 Sept. 1995 (DAO).

Porsild and Cody (1980) knew this species from a single site in the Mackenzie Mountains. Cody and Talbot (1978) reported a second site from adjacent to the Mackenzie Highway near the west end of Great Slave Lake. The specimens cited above are an extension of the known range in the Territory of about 250 kilometers northeast of the Mackenzie Highway site.

Potamogeton obtusifolius M.& K. (*P. porsildiorum* sensu Porsild and Cody 1980) – MACKENZIE: in small lake, Mile 38.35 Yellowknife Highway, *Thieret and Reich 8359*, 2 Aug. 1961 (DAO) (determined by R.R. Haynes); in shallow water at disturbed edge of small pool, Mile 45.55 Yellowknife Highway, *Thieret and Reich 7947*, 23 July 1961 (DAO) (determined by R.R. Haynes); small lake, Mile 12.75 Yellowknife Highway, *Thieret and Reich 7858*, 20 July 1961 (DAO) (determined by R.R. Haynes); KEEWATIN: small lake south of 74-1W, west of Bissett Lake, 63°45'25"N 95°34'30"W, *K.L. Reading s.n.,* 31 Aug. 1982 (DAO).

Porsild and Cody (1980) suggested that this species should be expected in the southern parts of the Precambrian Shield area. The specimens cited above confirm this and also extend the known range into central District of Keewatin. The first three specimens cited above were originally determined as *P. porsildiorum*, a species which now should be excluded from the *Flora of the Continental Northwest Territories*.

Potamogeton richardsonii (Benn.) Rydb. – MACKENZIE: lakes along highway east of Yellowknife, 62°31'00"N 113°46'00"W, *K.L. Reading s.n.*, Sept. 1982 (DAO).

The specimen cited above is intermediate between sites mapped by Porsild and Cody (1980) at the east and west ends of Great Slave Lake.

Potamogeton vaginatus Turcz., Giant Pondweed – MACKENZIE: lake along highway east of Yellowknife, 62°27'35"N 113°43'20"W, *K.L. Reading s.n.,* Oct. 1982 (DAO); northeast corner of sizeable lake 1.5 miles southeast of Ptarmigan Mine, east of Yellowknife, 62°30'30"N 114°10'30"W, *K.L. Reading s.n.,* 12 Sept. 1982 (DAO); lake along highway east of Yellowknife, 62°33'00"N 114°02'00"W, *K.L. Reading s.n.*, Sept. 1982 (DAO); lake beside road a few miles east of Cameron Falls, 62°31'00"N 113°41'00"W, *K.L. Reading, s.n.*, 18 Sept. 1982 (DAO); KEEWATIN: small

lake south of 74-1W, west of Bissett Lake, 63°45'25"N 95°34'30"W, *K.L. Reading s.n.*, 31 Aug. 1982 (DAO).

The nearest site to the Mackenzie sites listed above known to Porsild and Cody (1980) is from adjacent to the west end of Great Slave Lake, about 150 kilometers to the southwest. Porsild and Cody knew of only three sites in mainland District of Keewatin. The specimen from west of Bissett Lake is the northernmost yet known from that Territory.

POACEAE (GRAMINEAE)

Agrostis mertensii Trin. ssp. *mertensii* (*A. borealis* Hartm.), Red Bent Grass – MACKENZIE: moist sand over bedrock, north end of Liard Range, Nahanni National Park, 61°07'N 123°47'W, *S.S. Talbot T5024-B*, 15 July 1975 (DAO); poorly drained lower slope, Hole-in-the-Wall Lake, Nahanni National Park, 61°48'N 128°17'W, *S.S. Talbot T—5088-A*, 7 Aug. 1975 (DAO); sandy soil, NE shoreline of Hole-in-the-Wall Lake, Nahanni National Park, 61°47'02"N 127°14'41"W, *J.M. Line 2000-276*, 18 Aug. 2000 (DAO) and *J.M. Line 2000-272*, 20 Aug. 2000 (DAO).

The specimens cited above are from sites intermediate between sites mapped by Porsild and Cody (1980) adjacent to the Liard River and the Canol Road.

Arctagrostis latifolia (R.Br.) Griseb. sl., Polargrass – MACKENZIE: *Salix/Dryas* alpine tundra on west-facing slope near crest of mountain in Liard Range, Mackenzie Mountains, 60°31'40"N 123°46'48"W, *Sharp et al. 3247*, 11 Aug. 1994 (DAO).

The specimen cited above is the southernmost yet found in the Mackenzie Mountains and is an extension of the known range mapped by Porsild and Cody (1980) of about 80 kilometers to the southeast.

Danthonia spicata (L.) Beauv. (*D. intermedia* sensu Porsild and Cody 1980) – MACKENZIE: all specimens in DAO from southeastern District of Mackenzie previously labelled *D. intermedia* were revised to *D. spicata* by S. Darbyshire (1986).

This species was expected by Porsild and Cody (1980).

Deschampsia elongata (Hook.) Munro, Slender Hairgrass – KEEWATIN: west of Imikula Lake, 62°09'N 97°55'W, *K.L. Reading s.n.*, 11 Sept. 1983 (DAO) (determined by S. Darbyshire).

Cody (1996) reported this species in the Yukon Territory Flora as "Western North America; from Alaska to northern Mexico; in the Yukon Territory introduced at Dawson and White Horse Rapids but not seen in recent years."

Elymus canadensis L., Canada Wild Rye – MACKENZIE: N side of roadbank, Willowlake River winter road, 500 m W of Norman Wells pipeline Km 380, 62°43'N 123°05'W, *K.L. MacInnes 86-94*, 16 July 1986 (DAO).

Cody (1979), Porsild and Cody (1980) and McJannet et al. (1995) knew this rare species in the Northwest Territories only from the west end of Great Slave Lake and near Fort Liard on the Liard River. The specimen cited above is the northernmost yet known in the District of Mackenzie and is from some 250 kilometers north of the Fort Liard location.

Phalaris arundinacea L., Reed Canary Grass – MACKENZIE: sandy, calcareous soil with wet depressions, Old Pots Hotspring, 61°32'37"N 126°28'47"W, *J.M. Line 2000-377*, 24 Aug. 2000 (Nahanni National Park Herbarium, photo DAO).

The specimen cited above is an extension of the known range in the Territory of about 160 kilometers northwest of South Nahanni (Porsild and Cody 1980).

Poa arctica R.Br., Arctic Blue Grass – MACKENZIE: lichen-moss herbmat, Liard Range, Mackenzie Mountains, 60°31'N 123°46'W, *G. Brunner LR-5-12*, 11 Aug. 1994 (DAO).

The specimen cited above is the southernmost yet found in the Mackenzie Mountains and is an extension of the range mapped by Porsild and Cody (1980) of about 80 kilometers to the southeast.

Vahlodea atropurpurea (Wahlenb.) Fries ssp. *latifolia* (Hook.) A.E. Porsild, Mountain Hairgrass – MACKENZIE: at the hotspring, Hole-in-the-Wall Lake, 61°46'23"N 127°18'04"W, *J.M. Line et al. 2000-337*, 20 Aug. 2000 (DAO) (determined by S. Darbyshire).

Porsild and Cody (1980) knew this subspecies from only two localities in the Mackenzie Mountains, the nearest of which was collected by *L. Allison* [no field number] at 62°46'N 129°1'W on 30 July 1973 (DAO) about 130 kilometers to the northwest.

CYPERACEAE

Carex arcta Boott, Northern Clustered Sedge – MACKENZIE: along outflow stream on northeast side of lake, Hole-in-the-Wall Lake, Nahanni National Park, 61°47'02"N 127°14'41"W, *J.M. Line 2000-283*, 18 Aug. 2000 (DAO).

Cody (1979) and McJannet et al. (1995) considered this species rare in the Territory on the basis of a single specimen collected at Hjalmer Lake, 61°05'N 109°15'W (*G.W. Scotter 3021*, 27 July 1962 (DAO)). The specimen cited above is only the second record for the Territory (Porsild and Cody 1980). In the Yukon Territory it is known only in the southeast.

Carex disperma Dewey – MACKENZIE: floodplain near mouth of Prairie Creek, Deadman Valley, South Nahanni River, Nahanni National Park, 61°15'N 124°27'W, *G.W. Scotter 23378*, 1976 (DAO); in dark conifer woods near the hotspring, Hole-in-the-Wall Lake, Nahanni National Park, 61°46'23"N 127°18'04"W, *J.M. Line 2000-343*, 20 Aug. 2000 (DAO).

The first specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 70 kilometers northwest of South Nahanni; the second specimen is a further extension to the northwest of about 220 kilometers.

Carex hoodii Boott – MACKENZIE: hot springs area, Cantung, 62°05'N 128°15'W, *M.G. Duman 70-851*, 30 July 1970 (MICH, photo DAO).

This species which is new to the flora of the Continental Northwest Territories was unfortunately missed during the writing of that book (Porsild and Cody 1980). A photocopy was recently sent to the author by A. A. Reznicek.

Densely tufted perennial herb with fibrous roots; stems 30-80 roughened on the angles above, longer than the leaves; leaves 2 or 3 per stem, flat or channeled below, 1.5-3.5 mm wide with tight sheaths; spikes 4 to 8, densely aggregated, unstalked, with both male and female flowers, the male flowers inconspicuous toward the tips, bracts rudimentary or absent; perigynia egg-shaped, 3.4-5 mm long, 1.5-2.5 mm wide, convex and nerved above, concave and nerveless below, green, smooth, very short-stalked, finely toothed on the upper half, the beaks 1/3 the length of the bodies, bidentate; scales egg-shaped, equalling or slightly shorter than the perigynia, pointed, brown, with greenish midribs and translucent margins; achenes lense-shaped, smooth 1.8-2 mm long; stigmas 2.

Carex maritima Gunn. – KEEWATIN: marine clay exposed around *Potamogeton obtusifolius* Lake S of 74-1W, *K.L. Reading s.n.*, 31 Aug. 1982 (DAO).

Porsild and Cody (1980) knew this species from three sites adjacent to the Hudson Bay coast of continental District of Keewatin and one locality in the interior. The specimen cited above is the second found in the interior.

Carex microptera Mack. – MACKENZIE: in sedge meadow by hotsprings, Canada Tungsten Mine, Flat River, 61°58'N 128°15'W, *Cody and Spicer 17676*, 7 Aug. 1967 (DAO); hot springs area, Cantung, 62°05'N 128°15'W, *M.G. Duman 70-850*, 30 July 1970 (MICH, photo DAO) (determined by A. A. Reznicek).

The specimens cited above are the first known from the Northwest Territories. The nearest known sites are adjacent to the North Canol Road in the Yukon Territory. These specimens were originally determined as *C. macloviana* from which this species can be separated as follows:

A. Scale margins, perigynia tips, and dorsal suture margins noticeably white hyaline; perigynia wings darkened, contrasting with the body of the perigynia; achenes filling more than half of the perigynia ..... *C. macloviana*

A. Scale margins and perigynia tips not differentiated or narrow hyaline margined; perigynia wings concolorous with body of the perigynia, wings at most dark edged; achenes filling less than half of the perigynia ..... *C. microptera*

Carex petasata Dewey, Broad-wing Sedge – MACKENZIE: shale slide rock on S slope of Red Mt., Vicinity of Brintnell Lake, approx. 62°5'N 127°35'W, alt., 5800 ft., *Raup and Soper 9795*, 7 Aug. 1939 (GH, photo DAO) (determined by B. Boivin in 1979).

Porsild and Cody (1980) suggested that this species should be looked for in southwestern District of Mackenzie. It was later found by Cody (1996) as north in the Yukon Territory at the vicinity of Dawson. The specimen cited above was originally determined as *C. phaeocephala*.

Carex tenuiflora Wahlenb. – MACKENZIE: mossy shoreline, Hole-in-the-Wall Lake, 61°47'02"N 127°14'41"W, *J.M. Line 2000-278*, 19 Aug. 2000 (DAO).

The specimen cited above is an extension of the known range in Nahanni National Park of about 200 kilometers northwest of sites in the vicinity of Yohin Lake (Porsild and Cody 1980).

Eleocharis acicularis (L.) R.& S., Hair Grass – MACKENZIE: lowland *Equisetum fluviatile-Carex rostrata-Bryum pseudotriquetrum* community, Nahanni National Park, 61°53'N 126°14'W, *S. Talbot T6233-X-2*, 10 Aug. 1976 (DAO).

The specimen cited above which was previously reported by Cody et al. (1979) was unfortunately not included on the map in Porsild and Cody (1980).

Eleocharis quinqueflora (F. Hartm.) Schwartz (*E. pauciflora* (Lightf.) Link var. *fernaldii* Svens.) – MACKENZIE: at the hotspring, Hole-in-the-Wall Lake, 61°46'23"N 127°18'04"W, *J. M. Line 2000-341*, 20 Aug. 2000 (DAO).

Porsild and Cody (1980) knew this circumpolar species in the District of Mackenzie only from the vicinities of Great Bear Lake and Great Slave Lake.

Eriophorum viridi-carinatum (Engelm.) Fern. – MACKENZIE: *Potentilla fruiticosa-Anemone parviflora-Tofieldia glutinosa* community, Nahanni National Park, 61°36'N 125°49'W, *S. Talbot T6021-16*, 9 July 1976 (DAO).

The specimen cited above which was previously reported by Cody et al. (1979) was unfortunately not included on the map in Porsild and Cody (1980).

Kobresia myosuroides (Vill.) Fiori and Paol. – MACKENZIE: graminoid-*Dryas integrifolia*-moss alpine tundra, Liard Range, Mackenzie Mountains, 60°36'N 123°47'W, *G. Brunner LR-8-2*, 12 Aug. 1994 (DAO); dry ridge, E slope of Liard Range, Mackenzie Mountains, 60°36'N 123°48'W, *G. Brunner 191*, 12 Aug. 1994 (DAO).

The specimens cited above are the southernmost yet found in the western Northwest Territories. The nearest known site is about 100 kilometers to the northwest in Nahanni National Park (Porsild and Cody 1980). Nearby in extreme southeastern Yukon Territory it is known from the Kotaneelee Range (Cody, Kennedy, and Bennet 2000) and then is disjunct to the southern Canol Road.

Kobresia siberica Turcz. (*K. hyperborea* A. E. Porsild) – MACKENZIE: *Dryas integrifolia* alpine tundra, Liard Range, Mackenzie Mountains, 60°36'N 123°47'W, *G. Brunner LR-12-5*, 12 Aug. 1994 (DAO).

The specimen cited above is the southernmost yet found in the Northwest Territories. The nearest site to the north is in the South Nahanni River area at 61°21'N 124°20'W (Scotter and Cody 1974; Porsild and Cody 1980). To the west it is known from the La Biche River area at 60°32'N, 124°30'W, in the Yukon Territory (Cody et al. 1998), a site which is disjunct to west of longitude 136°W.

Scirpus validus Vahl, Common Great Bulrush – MACKENZIE: slow moving stream, Rat River on Taltson River SE of Great Slave Lake, 61°06'N 112°38'W, *B. Bromley 6*, 6 July 1972 (DAO); rooted in silt along margin of river, Jean River, Slave River Delta, 61°22'N 113°22'W, *W. J. Cody 14550*, 6 Aug. 1965 (DAO); common around edges beside pond in standing water, 22 km southwest of Mackenzie and Liard highway, *Chmielewski et al. 2232*, 22 June 1986 (CAN); wet

ground by buildings, Norman Wells, *Cody and Gutteridge 7835*, 7 Aug. 1953 (DAO); in mud flat in slough off the Mackenzie River near the campground in town, Fort Simpson, 61°51.65'N 121°20.7'W, *B. Bennett 98-490*, 13 Sept. 1998 (B. Bennett Herbarium, photo DAO).

Most of the specimens mapped as *S. validus* by Porsild and Cody (1980) have been revised to *S. acutus* (see Cody et al. 2001) for key. *Scirpus validus* should now be considered as rare in the Continental Northwest Territories (McJannet et al. 1995).

JUNCACEAE

Juncus balticus Willd. ssp. *alaskanus* (Hultén) A.E. Porsild – MACKENZIE: on sand spit east of camp, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 35-1*, 22 Aug. 1999 (DAO); KEEWATIN: east of Mountain Lake, 61°12'18"N 98°31'20"W, *K.L. Reading s.n.*, 19 July 1992 (DAO).

The first specimen cited above is from a site about 80 kilometers east of the east end of Great Bear Lake (Porsild and Cody 1980). The second specimen cited above is the first known from the Continental District of Keewatin. To the west the nearest sites known to Porsild and Cody (1980) were about halfway between the east end of Great Slave Lake and the Mackenzie/ Keewatin border.

Juncus filiformis L. – MACKENZIE: Old Pots Hotspring, 61°32'37"N 126°28'47"W, *J.M. Line 2000-373*, 24 Aug. 2000 (DAO); KEEWATIN: common everywhere around lakeshores, northwest of Mountain Lake, 61°13'05"N 98°37'35"W, *K.L. Reading s.n.*, 12 Aug. 1991 (DAO).

The first specimen cited above is new to the area between the Mackenzie River and the Yukon border in the western part of the Continental Northwest Territories (Porsild and Cody 1980). In the Continental District of Keewatin, Porsild and Cody knew this species from a single collection in the extreme southwest. The second specimen cited above is only the second known from that region.

LILIACEAE

Maianthemum trifolium (L.) Sloboda (*Smilacina trifolia* (L.) Desf.) – KEEWATIN: west of Mountain Lake, 61°12'09"N 98°39'00"W, *K.L. Reading s.n.*, 17 Aug. 1991 (DAO).

Porsild and Cody (1980) knew this taxon from only one locality in the Continental District of Keewatin just north of the Manitoba/Keewatin border. The specimen cited above is from a site northwest of that known by Porsild and Cody.

ORCHIDACEAE

Corallorhiza trifida Chat., Yellow coralroot – KEEWATIN: east of Mountain Lake, 61°12'18"N 98°31'20"W, *K.L. Reading s.n.*, 19 July 1992 (DAO).

The specimen cited above is only the second known from the Continental District of Keewatin. It is from a site intermediate between a site adjacent to Hudson Bay and sites west of the Mackenzie/Keewatin border.

Platanthera aquilonis Sheviak (*P. hyperborea* (L.) Lindl., *Habenaria hyperborea* (L.) R.Br.), Northern Green Orchid – MACKENZIE: growing in trees above Big Bend, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 32-1*, 23 July 1999 (DAO).

The specimen cited above is an extension of the known range in the Territory of about 80 kilometers to the northeast of a site adjacent to the eastern bay of Great Bear Lake (Porsild and Cody 1980).

Platanthera obtusata (Pursh) Lindl. (*Habenaria obtusata* (Pursh) Richards.), Northern Bog Orchid – KEEWATIN: Shayne Lake, 63°45'00"N 95°02'04"W, *K.L. Reading s.n.*, Aug. 1983 (DAO); wet sphagnum near water, south of east arm of Tyrell Arm of Yathkyed Lake area, 62°11'22"N 97°53'00"W, *K.L. Reading s.n.*, 13 July 1984 (DAO); Pebble Beach Lake, 62°22'00"N 97°30'28"W, *K.L. Reading s.n.*, 16 July 1985 (DAO); east of Bernier Lake, 61°23'46"N 98°20'00"W, *K.L. Reading s.n.*, 6 July 1992 (DAO).

Porsild and Cody (1980) knew this taxon in the District of Keewatin only from the extreme south and adjacent to the Hudson Bay coast. The specimens cited above are from sites intermediate between the Hudson Bay coast and sites west of the Mackenzie/Keewatin border.

SALICACEAE

Salix athabascensis Raup – MACKENZIE: montane *Larix laricina-Carex aquatilis-Campylium stellatum* community, Nahanni National Park, 61°42'N 126°02'W, *S. Talbot T6142-28*, 28 July 1976 (DAO).

The specimen cited above is from a site about 200 kilometers west of a site mapped by Porsild and Cody (1980) in the vicinity of Fort Simpson.

Salix lutea Nutt. – MACKENZIE: on banks of South Nahanni River opposite the base of Twisted Mtn., 61°12'N 123°41'W, *B.J.J. Meuleman M6058-1*, 25 July 1976 (DAO).

The specimen cited above which was previously reported by Cody et al. (1979) was not mapped by Porsild and Cody (1980). It is the only known collection from adjacent to the Liard River.

Salix polaris Wahlenb. (*S. polaris* Wahlenb. ssp. *pseudopolaris* (Flod.) Hultén), Snow-bed Willow – MACKENZIE: Paulatuk, 69°49'N 123°59'W, *C. Burn*, 11 Aug. 2001 (DAO).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 340 kilometers east of a site in the vicinity of Tuktoyaktuk. It is, however, known from Banks, Victoria and Melville islands to the north.

Salix rotundifolia Trautv. ssp. *rotundifolia* – MACKENZIE: in deep moss on granitic mountain, Mackenzie Mts., 5 miles SE of O'Grady Lake, 62°57'N 128°58'W, *W.J. Cody 16750*, 27 July 1967 (DAO); moist tundra, limestone mountain top, Mackenzie Mts., 10 miles NE of O'Grady Lake, 63°05'N 128°50'W, *W.J. Cody 16889*, 29 July 1967 (DAO); limestone, stony tundra slope, Mackenzie Mts., 17 miles NW of Little Divide Lake, 63°17'N 128°17'W, *W.J. Cody 16633*, 26 July 1967 (DAO) (determined by G. Argus).

The specimens cited above are the only ones known from the Northwest Territories and were unfortunately overlooked

during the writing of the *Flora of the Continental Northwest Territories* (Porsild and Cody 1980). This taxon should be added to the *Rare Vascular Plants in the Northwest Territories* (McJannet et al. 1995) In the Yukon Territory, it is only known in Ivvavik and Kluane National Parks.

BETULACEAE

Alnus crispa (Drylander ex Ait.) Pursh, Green Alder – KEEWATIN: creek into southeast corner of lake, Pebble Beach Lake, 62°21'40"N 97°31'02"W, *K.L. Reading s.n.*, 10 July 1985 (DAO).

The specimen cited above is the northernmost yet known in the Territory (Porsild and Cody 1980).

POLYGONACEAE

Koenigia islandica L., Iceland Koenigia – KEEWATIN: colour photograph, SE of Bissett Lake, 63°49'N 95°15'W, *K.L. Reading s.n.*, 1983 (DAO); west southwest of Bissett Lake, 63°49'N 95°05'W, *K.L. Reading s.n.*, 8 Aug. 1982 (DAO); in sink lake bottom, south of east end of Bissett Lake, 63°10'05"N 95°10'05"W, *K.L. Reading s.n.*, 16 Aug. 1982 (DAO); very wet mossy esker-base springs 8 miles south of east end of Bissett Lake, 68°41'50"N 95°16'82"W, *K.L. Reading s.n.*, 16 Aug. 1982 (DAO).

Porsild and Cody (1980) knew this taxon from only three localities in the Continental District of Keewatin, two adjacent to the coast of Hudson Bay and one south of the Arctic Circle.

Polygonum fowleri Robinson – MACKENZIE: common in fill along roadside, Bell Rock, 8 miles west of Ft. Smith, 60°01'N 112°06'W, *Cody and Loan 4391*, 13 July 1950 (DAO) (determined by Wolf and McNeill 1983).

This specimen was originally determined as *Polygonum aviculare*. It should now be added to the flora of the District of Mackenzie and the Continental Northwest Territories. *Polygonum fowleri* can be separated from *P. aviculare* by its smooth or somewhat roughened, but never papillose achenes.

Polygonum hudsonianum (Wolf and McNeill) Hinds (*P. caurianum* Robinson ssp. *hudsonianum* Wolf and McNeill) – KEEWATIN: James Bay, North Twin Island, 53°18'N 80°00'W, *T.H. Manning s.n.*, 25 July 1973 (DAO); very wet gravel of coastal beach, mouth of McConnell River, 60°50'N 94°25'W, *K.L. MacInnes 721*, 14 Aug. 1968 (DAO); MACKENZIE: Reindeer Station, Mackenzie River Delta, East Branch, *A.E. Porsild s.n.*, 1 Sept. 1935 (DAO) (determined by H. Hinds 1994).

These specimens, which were previously identified as *Polygonum caurianum,* were revised to *P. hudsonianum* by H. Hinds. To the south this species is known from Quebec to Saskatchewan.

Polygonum ramosissimum Michx. – MACKENZIE: along tractor trail through bush, west of Le Grand Detour, Slave River, 60°21'N 112°44'W, *W.J. Cody 13932*, 25 July 1965 (DAO) (determined by Wolf and McNeill 1983).

This native plant which was originally determined as *Polygonum aviculare s.l.* has not previously been reported as occuring in the Continental Northwest Territories. It may be distinguished by its erect or ascending striate stems 30 to 100 or more cm tall, with usually thin, lanceolate to linear leaves 1 to 6 cm long, tapering at each end.

CHENOPODIACEAE

Corispermum hookeri Mosyakin, Bugseed – MACKENZIE: in dry sand near shoreline, sand hills on south shore of Mackenzie River about 16 miles downstream from Fort Simpson, 61°58'N 121°45'W, *Cody and Matte 8944*, 25 July 1955 (DAO, PARATYPE); (immature, probably *C. hookeri*), occasional in disturbed sand along roadside on mainland about 1 mile south of Fort Simpson island, 61°52'N 121°22'W, *Cody and Matte 9130*, 3 Aug. 1955 (DAO); (not completely mature, probably *C. hookeri*), rare in disturbed ground of road cut down to river at upper end of island, Fort Simpson, 61°52'N 121°22'W, *Cody and Matte 9335*, 11 Aug. 1955 (DAO); *Melilotus-Salix* sand bar on island in Liard River, 60°03'24"N 123°50'25"W, *Kubiw et al. 1014*, 17 Aug. 1994 (DAO).

For comments see below under *C. ochotense*.

Corispermum ochotense Ignatov – MACKENZIE: riverbank, rare, E bank of Mackenzie River, Norman Wells, 65°17'N 126°47'W, *N.J. Walker 2386*, 18 Aug. 1974 (DAO); beach ridge-sandy-with *Populus tremuloides*, 13.0 km WSW of Norman Wells, 65°14'N 127°01'W, *N.J. Walker 2303*, 10 Aug. 1974 (DAO); eroding heavy soil on slope by airstrip, Norman Wells, *Cody and Gutteridge 7466*, 22 July 1953 (DAO); rare on gravel beach of Mackenzie River, Royal Canadian Corps Signals Transmitters, 5 miles upstream from Norman Wells, *Cody and Gutteridge 7603*, 27 July 1953 (DAO); on the section of slit beach, Aklavik River near Aklavik, *M.E. Oldenburg 48-1241*, (GH).

The DAO specimens cited above, with the exception of the Kubiw specimen from the Liard River which is an extension of the known range of about 200 kilometers from Fort Simpson, under both *C. hookeri* and *C. ochotense* were mapped by Porsild and Cody (1980) as *C. hysopifolium*, a species which Mosyakin (1995) reported is restricted to a small area in southeastern Europe and adjacent parts of western Asia. *Corispermum hysopifolium* should be deleted from the flora of the Continental Northwest Territories and *C. hookeri* and *C. ochotense* should be added to that flora. Both of these should be considered for addition to the *Rare Vascular Plants of the Northwest Territories* (McJannet et al. 1995).

Corispermum villosum Rydb. (*C. orientale* var. *emarginatum* sensu Cody, MacInnes, Cayouette, and Darbyshire 2000).

This species was reported as an introduction along the Norman Wells Pipeline. It can be separated from *C. hookeri* and *C. ochotense* as follows:

A. Fruits wingless or wing less than 0.1 mm wide; leaves linear or linear-oblanceolate; plants much branched, up to 30 cm high ..... *C. villosum*

A. Fruits usually winged, the wing 0.2-0.3 broad (sometimes lacking in *C. hookeri*);

leaves linear, linear spatulate or lanceolate; plants to 20 cm high
B. Fruits 3.5-4.5 mm long; leaves lanceolate or linear-lanceolate; plants much branched, up to 20 cm high ..... *C. hookeri*
B. Fruits 2.8-3.2 mm long; leaves linear or linear-spatulate; small branched plants up to 10 cm high ..... *C. ochotense*

Suaeda calceoliformis (Hook.) Moq., Sea-blite – MACKENZIE: saline clay, Walker Bay, Kent Peninsula, *G. Loh 1*, 9 July 1996 (DAO); drying saline mudflats, same locality, *G. Loh 2*, 31 July 1996 (DAO).

This is a rare species in the Northwest Territories north of treeline (McJannet et al. 1995). On the Arctic Coast it was known only from Eskimo Lakes, Franklin Bay, Lower Brock Lagoon and the west end of Coronation Gulf. The specimens cited above are an extension of the known range eastward some 225 kilometers.

CARYOPHYLLACEAE

Minuartia rossii (R.Br.) Graehm., Ross' Stichwort – MACKENZIE: camp area, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 3-1*, 6 July 1999 (DAO); same area, *K.L. Reading 31-1*, 21 July 1999 (DAO).

The specimens cited above are from a site about 110 kilometers east of a site adjacent to the northeastern peninsula of Great Bear Lake and 120 kilometers south of a site in the vicinity of Coppermine.

Minuartia rubella (Wahlenb.) Graebn. ex Asch. and Graebn., Boreal Sandwort – MACKENZIE: Big Bend Area, Coppermine River approx. 66°52'N 115°50'W, *K.L. Reading 21-1*, 11 July 1999 (DAO); same area, *K.L. Reading 39-7*, Sept. 1999 (DAO); same area, *K.L. Reading 20*, 10 Oct. 1998 (DAO).

The specimens cited above are from an area about 50 kilometers east of the bay at the east end of Great Bear Lake and about 120 kilometers south of a site in the vicinity of Coppermine.

Silene taimyrensis (Tolm.) Bocquet (*Melandrium taimyrense* Tolm.) – KEEWATIN: dry arkose scarp-scree and ledges, N of 30-mile Lake, 63°40'38"N 96°04'00"W, *K.L. Reading s.n.*, 22 July 1981 (DAO).

Porsild and Cody (1980) knew this species only as far east as the Mackenzie/Keewatin border.

Silene uralensis (Rupr.) Bocquet ssp. *ogilviensis* (A.E. Porsild) Brunton – MACKENZIE: shallow soil over rock on tundra hilltop, Mile 44E Canol Road, Mackenzie Mountains, *Cody and Gutteridge 7713*, 1 Aug. 1953 (DAO) (determined by J.K. Morton); Lower Brock Lagoon, Bluenose Lake Area, Melville Hills Region, 69°31'N 123°13'W, *G.W. Scotter 90-563*, 29 July 1990 (DAO) (determined by J. K. Morton).

Cody et al. (2002) extended the known range of this endemic taxon northeast to the southern Richardson Mountains and north to the British Mountains from sites adjacent to the Dempster Highway in the Yukon Territory. The specimens cited above extend the known range eastward into the former District of Mackenzie to the central Mackenzie Mountains and in the north along the Arctic Coast to longitude 123°13'W. *Silene uralensis* ssp. *ogilviensis* should be added to the list of rare taxa in the Territory (McJannet et al. 1995).

Stellaria borealis (Ledeb.) Bong. (*S. calycantha* sensu Porsild and Cody 1980) – MACKENZIE: in moss on wet beach margins, vicinity of Daring Lake, 64°52'N 111°37'W, *McNair and O'Brien 25*, 16 Aug. 1994 (DAO) (determined by J.K. Morton); KEEWATIN: in tallish willow copses, west end of "Jaeger" Lake (south of Yathkyed Lake, 60°46'N 110°16"W), *K.L. Reading 85-33*, mid-August 1985 (DAO); willow copses at west end of Yathkyed Lake, *K.L. Reading 85-34*, mid-August 1985 (DAO).

The first specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 215 kilometers north of the east end of Great Slave Lake and 350 kilometers southeast of the east end of Great Bear Lake. The second two specimens are from sites between two locations in the extreme southeast of the District of Mackenzie mapped by Porsild and Cody (1980).

Stellaria crassifolia Ehrh., Thick-leaved Starwort – MACKENZIE: Coppermine River "Big Bend" Area, 66°52'38"N 115°50'W, *K.L. Reading 37*, 15 Sept-10 Oct. 1998 (DAO); KEEWATIN: uncommon in deep crevices between shoreline boulders, east slope of Grayling Lake, 63°49'50"N 95°25'00"W, *K.L. Reading s.n.*, 8 Aug 1982 (DAO); sedge pool near Bissett Creek, 63°45'26"N 95°27'54"W, *K.L. Reading s.n.*, 14 Aug. 1981 (DAO).

The first specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 80 kilometers east of a site adjacent to the northeast end of Great Bear Lake. The second two specimens were from areas intermittent between sites adjacent to longitude 100°W and the Hudson Bay coast.

RANUNCULACEAE

Caltha natans Pall., Floating Marsh-marigold – KEEWATIN: northeast of Cullaton Lake, 61°20'35"N 98°19'10"W, *K.L. Reading s.n.*, Sept. 1987 (DAO).

Porsild and Cody (1980) knew this taxon in the District of Keewatin from only two sites in the south of the Territory. The specimen cited above is a slight extension of the range northeast of the western site.

Caltha palustris L. ssp. *arctica* (R.Br.) Hultén, Marsh-marigold – KEEWATIN: NW corner of Bissett Lake, 63°52'45"N 95°17'48"W, *K.L. Reading s.n.*, 8 Aug. 1983 (DAO).

Porsild and Cody (1980) knew this taxon in the Continental District of Keewatin from two localities in the central area and one adjacent to the Arctic Coast. Cody (1996) cited a third collection from a site to the northeast of the northern specimen. The new specimen documented above from near the Arctic Circle is from a site intermediate between those previously reported.

Ranunculus aquatilis L. var. *hispidulus* E. Drew (*R. trichophyllus* Choix var. *hipidulus* (E. Drew) W.B. Drew) – MACKENZIE: rare in shallow marly slough, Hunter Bay, McTavish Arm, Great Bear Lake, 66°12'N

117°39'W, *A.E. and R.T. Porsild 5299*, 9-10 Aug. 1928 (CAN, photo DAO).

This specimen which has laminate as well as filliform-dissected leaves was cited by Benson (1948) in his monograph of North American Ranunculi. It should however probably be included in the synonomy of var. *aquatilis*.

Ranunculus flammula L., Creeping Spearwort – MACKENZIE: mud bank built up by the lake along the shore, Oxbow Lake, Virginia Falls, Nahanni National Park, 61°38'N 125°42'W, *L.N. Carbyn 23*, 2 Aug. 1974 (DAO).

This specimen which was reported from Nahanni National Park (Cody et al. 1979) was unfortunately not included on the map in Porsild and Cody (1980). The nearest site recorded by Porsild and Cody (1980) was in the vicinity of Fort Simpson.

Ranunculus flammula L. var. *filiformis* (Michx.) Hook. – KEEWATIN: 1/4 mile north of camp on Bissett Lake, 63°47'00"N 95°28'30"W, *K.L. Reading s.n.*, 12 Aug. 1982 (DAO).

The specimen cited above is the fifth known in mainland District of Keewatin and the northernmost yet found in that Territory.

Ranunculus nivalis L., Snow Buttercup – MACKENZIE: Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 17-2*, 10 July 1999 (DAO).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 120 kilometers southeast of a site west of Coppermine.

Ranunculus pallasii Schlecht, Pallas' Buttercup – KEEWATIN: flooded marsh south of Deep Bay of Kazan River, 63°42'02"N 95°37'00"W, *K.L. Reading s.n.*, 3 Aug. 1982 (DAO); small tundra pond, north of TK camp on Bissett Lake, 63°47'22"N 95°28'00"W, *K.L. Reading s.n.*, 17 Aug. 1982 (DAO).

Porsild and Cody (1980) knew this species in mainland District of Keewatin only from coastal Hudson Bay in the vicinity of Rankin Inlet. Additional specimens from the Arctic Coast region were added by Cody (1996). The specimens cited above are the first known from the interior of Continental District of Keewatin.

Ranunculus pygmaeus Wahlenb., Dwarf Buttercup – KEEWATIN: in sink lake bottom, south of east end of Bissett Lake, 63°42'55"W 95°10'05"W, *K.L. Reading s.n.*, 16 Aug. 1982 (DAO); TK camp peninsula, Bissett lake, 63°46'38"N 95°26'12"W, *K.L. Reading s.n.*, 17 Aug. 1982 (DAO).

Porsild and Cody (1980) knew this species from only four localities in the southern half of the Continental District of Mackenzie. An additional site from the vicinity of Wager Bay was added by Cody et al. (1989). The specimens cited above extend the known range in the interior northward.

Ranunculus sulphureus Sol., Sulpher Buttercup – MACKENZIE: George Lake, 65°57'20"N 107°30'00"W, *K.L. Reading s.n.*, 12 Aug. 1988 (DAO).

Cody et al. (1984) reported a specimen from the Bathurst Inlet region which was the first record of this circumpolar arctic-alpine species in the Continental Northwest Territories east of the Mackenzie River. The specimen cited above is from a locality south of Bathurst Inlet.

PAPAVERACEAE

Papaver macounii Greene ssp. *discolor* (Hultén) Randel (*P. keelei* Porsild) – KEEWATIN: 6 miles south of 30-m Lake, 63°33'12"N 95°53'50"W, *K.L. Reading s.n.*, 20 Aug. 1982 (DAO).

The specimen cited above is new to the Continental District of Keewatin and is an extension of the known range east of the west end of Great Bear Lake.

BRASSICACEAE (CRUCIFERAE)

Descurainia incisa (Engelm. ex Gray) Britton var. *incisa* – MACKENZIE: scattered along roadside, Port Radium: Eldorado Mine, 66°05'N 118°03'W, *W.J. Cody 2792*, 21 July 1949 (DAO) (determined by G. A. Mulligan).

This specimen was originally determined as *D. richardsonii* (synonym of *D. incana*) and mapped by Porsild and Cody (1980) under that name. It is new to the Flora of the Northwest Territories where it was probably introduced.

Draba alpina L., Alpine Draba – MACKENZIE: Camp area, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 2-1C*, 6 July 1999 (DAO) (determined by G. A. Mulligan).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 120 kilometers south of the vicinity of Coppermine.

Draba cinerea Adams – MACKENZIE: Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 39-4*, Sept. 1999 (DAO); camp area, same area, *K.L. Reading 2-1A*, 6 July 1999 (DAO) (determined by G. A. Mulligan).

The specimens cited above are an extension of the known range in the Territory (Porsild and Cody 1980) of about 50 kilometers northeast of a site adjacent to the east end of Great Bear Lake and about 120 kilometers south of Coppermine.

Draba glabella Pursh – MACKENZIE: camp area, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 2-1B*, 6 July 1999 (DAO) (determined by G. A. Mulligan).

The specimen cited above is an extension of the known range in the Territory of about 50 kilometers northeast of a site adjacent to the east end of Great Bear Lake and about 120 kilometers south of Coppermine (Porsild and Cody 1980).

Draba lactea Adams – MACKENZIE: common on taluses, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 14-1A*, 8 July 1999 (DAO) (determined by G. A. Mulligan).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 120 kilometers south of the vicinity of Coppermine.

Draba stenoloba Ledeb. – MACKENZIE: alpine *Salix-Carex-Artemisia arctica* community, Nahanni National Park, *S. Talbot T6157-32*, 30 July 1976 (DAO); Canol Road Mile 192, 63°34'N 129°12.5'W, *L. and G.P. Kershaw 3748*, 3 July 1977 (DAO); Mile 198 Canol Road, 63°30.5'N 129°16.5'W, *L. and G.P. Kershaw 772*, 17 July 1977 (DAO); Canol Road Mile 212-213, 63°24.5'N 129°38'W, *L. and G.P. Kershaw*

1590, 28 June 1972 (DAO); Canol Road 216, 63°22'N 129°42'W, *L. and G.P. Kershaw 2243*, 21 June 1977 (DAO); Canol Road 221-222, 63°18.5'N 129°47'W, *L. and G.P. Kershaw 2413*, 16 June 1977 (DAO) (determined by G. A. Mulligan).

The first specimen cited above was reported by Cody et al. (1979) but was not mapped by Porsild and Cody (1980). The remaining were not incorporated into DAO until 1983. *Draba stenoloba* should be added to the Flora of Continental Northwest Territories.

Erysimum coarctatum Fern.

Cody et al. (2000) reported the following information on this taxon: "Specimens from the Yukon Territory, Continental Northwest Territories, Alberta and British Columbia, previously determined as *E. inconspicuum* (S. Wats.) MacM. have been revised to *E. coarctatum* by G. A. Mulligan. These two species can be separated as follows:

A. Limb of petals 2.5-3 mm long, 1.5-2 mm broad; fruiting raceme elongate (up to 2 or 3 dm long) and open; siliques about 1 mm broad; seeds 1-1.3 mm long *E. inconspicuum*

A. Limb of petals 4.5-6 mm long, 2-3 mm broad; fruiting raceme crowded and corymbiform at summit; siliques 1.5-2 mm broad; seeds 1.6-2 mm long *E. coarctatum*

Erysimum inconspicuum should be deleted from the floras of the Yukon Territory and Continental Northwest Territories.

Subularia aquatica L. ssp. *americana* Mulligan and Calder, Awlwort – MACKENZIE: Cameron River about 28 miles east of Yellowknife, *K.L. Reading s.n.*, 17 Aug. 1995 (DAO); in Landing Bay of Prosperous Lake, east of Yellowknife, 62°32'05"N 114°09'20"W, *K.L. Reading s.n.*, Sept. 1982 (DAO).

Cody (1996) knew this species in the District of Mackenzie from only five localities: Tsu Lake, Great Bear Lake (Porsild 1943), Indin Lake, Yellowknife and Le Haise Lake. The specimens cited above are from sites intermediate between Yellowknife and Le Haise Lake (61°58'N 106°20'W).

CRASSULACEAE

Crassula aquatica (L.) Schoenl. (*Tillaea aquatica* L.), Pigmyweed – MACKENZIE: north shore of Landing Bay, Prosperous Lake, 62°36'N 114°12'W, *K.L. Reading s.n.*, 18 Sept. 1982 (DAO).

Porsild and Cody (1980) knew this species only from Yellowknife where it was first collected in 1949 (*Cody 3511* DAO) and later in 1953 (*Cody and Gutteridge 7318* DAO). These collections from very shallow water in flats of a bay by the old Yellowknife townsite resulted in the publication entitled "A history of *Tillaea aquatica* in Canada and Alaska" (Cody 1954). The specimen cited above is from a site a short distance northwest of Yellowknife. The nearest sites known to Porsild and Cody were in southern British Columbia, adjacent to the Alaskan Coast west of longitude 135°W, northwest of Thunder Bay in Ontario and one adjacent to the east coast of James Bay in Quebec. Since then however it has been reported in extreme southern Yukon Territory (Cody et al. 2002).

SAXIFRAGACEAE

Chrysosplenium tetrandrum (Lund) Fries, Northern Golden Saxifrage – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'W, *K.L. Reading 22*, 10 Oct. 1998 (DAO).

The specimen cited above is from a site about 120 kilometers south of the vicinity of Coppermine, 80 kilometers east of Great Bear Lake and 80 kilometers north of a site south of the Arctic Circle (Porsild and Cody 1980).

Parnassia kotzebuei Cham. and Schlecht – KEEWATIN: stream east of Kazan River north of Big Bend, 63°46'58"N 95°36'00"W, *K.L. Reading s.n.*, 7 Aug. 1983 (DAO); along sandy lakeshore, SSW of Bissett Lake, 63°41'28"N 95°35'15"W, *K.L. Reading s.n.*, 28 Aug. 1982 (DAO); south of east end of Bissett Lake, 63°44'00"N 95°10'00"W, *K.L. Reading s.n.*, 15 Aug. 1982 (DAO); stony lake shoreline, west southwest of Bissett Lake, 63°44'00"N 95°35'10"W, *K.L. Reading s.n.* 4 Aug. 1982 (DAO).

Porsild and Cody (1980) knew this taxon from only four sites in southern Continental District of Keewatin. The specimens cited above are now the northernmost yet found in that Territory.

Parnassia palustris L. var. *neogaea* Fern. – KEEWATIN: stream east of Kazan River north of Big Bend, 63°46'58"N 95°36'00"W, *K.L. Reading s.n.*, 7 Aug. 1983 (DAO).

Porsild and Cody (1980) knew this taxon from only four localities in the extreme south of the Continental District of Keewatin. The specimen cited above is the northernmost yet found in that Territory.

Saxifraga caespitosa L. ssp. *uniflora* (R.Br.) Porsild, Tufted Saxifrage – KEEWATIN: Andrews Lake, 63°59'05"N 94°51'00"W, *K.L. Reading s.n.*, 3 July 1981 (photo DAO).

Porsild and Cody (1980) knew this taxon from a single locality in the Continental District of Keewatin in the vicinity of Baker Lake. The photo cited above is from a site west of Baker Lake.

Saxifraga cernua L., Nodding Saxifrage – MACKENZIE: by creek, local, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 19-1*, 10 July 1999 (DAO).

The specimen cited above is from a site about 120 kilometers south of Coppermine and a site adjacent to the southeastern bay of Great Bear Lake, about 90 kilometers to the southwest (Porsild and Cody 1980).

Saxifraga foliolosa R.Br. – KEEWATIN: Washaneepisuki Lake, 62°12'04"N 97°50'40"W, *K.L. Reading s.n.*, 4 Aug. 1984 (DAO); east of Bissett Lake, 63°48'10"N 95°10'00"W, *K.L. Reading s.n.*, 20 July 1982 (DAO).

Porsild and Cody (1980) knew this species in Continental District of Keewatin from only three sites adjacent to the Hudson Bay coast and one adjacent to longitude 100°W. The specimens cited above are from intermediate sites.

Saxifraga hieracifolia Waldst. and Kit. – KEEWATIN: southwest of 74-1W of Bissett Lake, 63°51'00"N 95°34'55"W, *K.L. Reading s.n.*, 31 Aug. 1982.

Porsild and Cody (1980) knew this taxon south of the Arctic Circle in the Continental District of Keewatin from only one site at about latitude 63°N just east of longitude 100°W.

Saxifraga hirculus L., Yellow Marsh Saxifrage – MACKENZIE: common in wet area, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 29-1*, 21 July 1999 (DAO); Big Bend Area, Coppermine River, 66°52'38"N 150°50'W, *K.L. Reading 23*, 15 Sept.-10 Oct. 1998 (DAO).

This is a common species adjacent to the arctic coast in the Territory (Porsild and Cody 1980). The nearest collection site to the specimens cited above is adjacent to Coppermine about 120 kilometers to the north. To the west the nearest sites are adjacent to two bays near the west end of Great Bear Lake.

Saxifraga nelsoniana D. Don ssp. *porsildiana* (Calder and Savile) Hultén (*S. punctata* L. ssp. *porsildiana* Calder and Savile) – MACKENZIE: rare – shoreline with *Chrysosplenium*, Big Bend Area, Coppermine River, approx. 66°62'N 115°50'W, *K.L. Reading 24-1*, 14 July 1999 (DAO); KEEWATIN: TK camp peninsula, Bissett Lake, 63°46'38"N 95°26'12"W, *K.L. Reading s.n.*, 17 July 1982 (DAO).

The first specimen cited above is intermediate between sites mapped by Porsild and Cody (1980) adjacent to the east end of Great Bear Lake and Coronation Gulf. Porsild and Cody (1980) knew this species from four sites south of the Arctic Circle, two on each side of longitude 100°W in the Continental District of Keewatin. The second specimen cited above is the easternmost yet found in that Territory.

Saxifraga nivalis L., Alpine Saxifrage – MACKENZIE: turfy wet gravel, rare, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 18-1*, 10 July 1999 (DAO).

The specimen cited above is from a site intermediate between Coppermine, about 120 kilometers to the north and sites adjacent to the east end of Great Bear Lake (Porsild and Cody 1980).

ROSACEAE

Potentilla hyparctica Malte sl. – MACKENZIE: abundant in wet gravel fens, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 23-1*, 12 July 1999 (DAO); same locality, *K.L. Reading 16*, 10 Oct. 1998 (DAO).

The specimens cited above are from a site about 120 kilometers south of the vicinity of Coppermine and about 80 kilometers east of a site adjacent to eastern Great Bear Lake (Porsild and Cody 1980).

Potentilla nivea L. – KEEWATIN: Big Bird Lake, 62°17'38"N 97°39'15"W, *K.L. Reading s.n.*, 25 June 1985 (DAO).

Porsild and Cody (1980) knew this taxon from only three sites in the Continental District of Keewatin. The specimen cited above is a slight extension of the known range to the southeast.

Potentilla tridentata Sol., Three-toothed Cinquefoil – MACKENZIE: Upper Snowdrift River area, approx. 62°25'N 108°45'W, *K.L. Reading s.n.*, 26 July 1995 (DAO); occasional under aspen on beach ridge, Hill Island Lake, 60°27'N 109°49'W, *Ovenden and Rowe 388*, 20 July 1977 (DAO); gravelly soil on top of treeless hill, Small Tree Lake, 61°N 105°W, *Maini and Swan 467*, 19 July 1961 (DAO).

Cody (1956) reported the first substantiated record of this species in the District of Mackenzie. Scotter (1966) reported the second known locality in that area. The specimens cited above extend our knowledge of the range in southern District of Mackenzie, including the northernmost site yet known in the Upper Snowdrift River area.

Rubus arcticus L. ssp. *acaulis* (Michx.) Forke (*R. acaulus* Michx.) – KEEWATIN: east of Mountain Lake, 61°12'18"N 98°13'20"W, *K.L. Reading s.n.*, 19 July 1992 (DAO).

Porsild and Cody (1980) knew this taxon from only two sites in southwestern Continental District of Mackenzie. The specimen cited above is from a site intermediate between the sites mapped by Porsild and Cody (1980).

Spiraea beauverdiana Schneid., Spiraea – MACKENZIE: occasional on a sparsely vegetated meadow, Horton River, 69°37'N 126°50'W, *G.W. Scotter 101014*, 4 July 1995 (DAO).

Porsild and Cody (1980) gave the general distribution "An Amphi-Beringian species common in Alaska and Yukon Territory, reaching the Arctic Coast east of the Mackenzie Delta, but thus far not otherwise reported from east of the Mackenzie Valley". The specimen cited above is the easternmost yet found in the Canadian Arctic and is an extension of the known range from the Anderson River (69°16'N 128°15'W, *W.J. Cody 12589* (DAO), 69°20'N 128°13'W, *G.W. Scotter 12589* (DAO)) of some 50 kilometers to the Horton River.

FABACEAE (LEGUMINOSAE)

Astragalus australis (L.) Lam. (*A. aboriginum* Richards.), Indian Milk-vetch – MACKENZIE: rare, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 13-1*, 8 July 1999 (DAO).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 150 kilometers northeast of a site adjacent to the south side of Great Bear Lake.

Medicago sativa L. ssp. *falcata* (L.) Arcangeli var. *falcata*, Yellow Alfalfa – MACKENZIE: Fort Simpson, 61°51'N 121°20'W, *B. Bennett 98-441*, 13 Sept. 1998 (DAO) (determined by E. Small).

The specimen cited above is the first record of this variety growing wild in the Continental Northwest Territories.

Melilotus alba Desr., White Sweet Clover – MACKENZIE: *Populus balsamifera/Salix* thicket, Fort Liard Region, 60°09'N 123°43'W, *R. Mueller FTL-80-2*, 17 Aug. 1994 (DAO).

Porsild and Cody (1980) stated that this species was an "introducted roadside weed common in the upper Mackenzie

Valley". Additional DAO collections from the Liard River are as follows: at edge of garden, Fort Liard, 60°14'N 123°28'W, *Cody and Spicer 11761*, 28 July 1961; Nahanni Butte Village, 61°03'N 123°24'W, *G.W. Scotter 12850*, 5 July 1970; and rough cleared ground, Fort Simpson, 61°51'N 121°22'W, *Cody and Matte 8644*, 7 July 1955.

Oxytropis arctica R.Br. – MACKENZIE: drumlin SE of camp, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 15-1*, 9 July 1999 (DAO).

The specimen cited above is from a site about 120 kilometers south of one previously known from the vicinity of Coppermine (Porsild and Cody 1980).

Oxytropis deflexa (Pall.) DC. ssp. *foliolosa* (Hook.) Cody (var. *foliolosa* (Hook.) Barneby – MACKENZIE: calcareous soil, among alders at edge of lakeside prairie, Uplands Lake, 62°27'30"N 113°42'00"W, *K.L. Reading s.n.*, 29 Aug. 1981 (DAO).

Porsild and Cody (1980) knew the nearest sites of this taxon in the Mackenzie Mountains to the west and adjacent to the Arctic Coast to the north.

VIOLACEAE

Viola adunca J.E. Smith, Hook-spur Violet – MACKENZIE: hotspring area diverse in ferns, mosses and graminoids, Hole-in-the-Wall Lake, Nahanni National Park, 61°46'23"N 127°18'04"W, *J.M. Line 2000-327*, 20 Aug. 2000 (DAO); KEEWATIN: west of Henik Lake, 61°26'10"N 97°55'46"W, *K.L. Reading s.n.*, 18 July 1992 (DAO).

The first specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 230 kilometers northwest of a site in the vicinity of Nahanni Butte. The second specimen is the first record for the Continental District of Keewatin.

Viola epipsila Ledeb. ssp. *repens* (Turcz.) Becker, Dwarf Marsh Violet – MACKENZIE: thicket *Alnus incana-Salix lucida* ssp. *lasiandra*, Fort Liard region 60°17'N 123°21'W, *G. Brunner FLT-30-74*, 16 Aug. 1994 (DAO); KEEWATIN: north of Cullaton Lake, 61°25'50"N 98°20'02"W, *K.L. Reading s.n.*, 6 July 1992 (DAO); south of east arm of Tyrell Arm of Yathkyed Lake, 62°12'00"N 97°50'35"W, *K.L. Reading s.n.*, 3 Aug. 1984 (DAO); Big Bird Lake, 62°17'06"N 97°37'25"W, *K.L. Reading s.n.*, 29 June 1985 (DAO).

This species was not included in the *Rare Vascular Plants in the Northwest Territories* (McJannet et al. 1995) because it is a widespread Amphi-Beringian species. The first specimen cited above is the southernmost yet found in the Northwest Territories. The nearest site to this collection in the Territory is at a small unnamed lake 9 miles SES of Hole-in-the-Wall Lake (61°42'N, 127°10'W) in northern Nahanni National Park. Cody (1996) reported a range extension to the vicinity of Burnside River southwest of Bathurst Inlet. The three Keewatin specimens cited above are a further extension to the east. This species is also known from the Thunder Bay region in northwestern Ontario.

Viola renifolia Gray var. *brainerdii* (Greene) Fern., Kidney-leaved Violet – KEEWATIN: northeast of Mountain Lake, 61°12'00"N 98°32'00"W, *K.L. Reading s.n.*, 19 July 1992 (DAO).

Cody (1996) reported the first record of this species in the Continental District of Keewatin. The specimen cited above is an extension of the known range to the west from longitude 97°40'W.

ELAEAGNACEAE

Shepherdia canadensis (L.) Nutt., Soapberry – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'00"W, *K.L. Reading 26*, 15 Sept.-10 Oct. 1998 (DAO).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 120 kilometers east and northeast of sites adjacent to the east end of Great Bear Lake.

ONAGRACEAE

Epilobium anagalidifolium Lam. – MACKENZIE: amphibolite ridge on Cameron Falls road east of Yellowknife, 62°30'20"N 114°13'00"W, *K.L. Reading s.n.*, 10 Oct. 1981 (MO, photo DAO).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 600 kilometers east of a site adjacent to Nahanni National Park.

Epilobium arcticum Samuelss., (*E. davuricum* Fisch. var. *arcticum* (Samuelss.) Polunin) – KEEWATIN: fresh boils, SSW of Bissett Lake, 63°49'41"N 95°15'38"W, *K.L. Reading s.n.*, Aug. 1982 (MO, photo DAO); scattered population in clay boils, 11 miles south of east end of Bissett Lake, 63°47'54"N 95°27'40"W, *K.L. Reading s.n.*, 18 Aug. 1982 (MO, photo DAO); fresh boils, E of Kazan Falls, 63°43'N 95°43'W, *K.L. Reading s.n.*, 30 Aug. 1982 (MO, photo DAO); 6 miles south of east end of 30-mile Lake, 63°35'28"N 95°50'00"W, *K.L. Reading s.n.*, 20 Aug. 1982 (MO, photo DAO).

Porsild and Cody (1980) knew this species in the District of Keewatin only from near the Hudson Bay coast and in the extreme north. The specimens cited above extend the known range in the Territory about 215 kilometers west of the Hudson Bay sites.

Epilobium davuricum Fisch. – KEEWATIN: wet rock polygons northwest of Bissett Lake, 63°49'45"N 95°24'08"W, *K.L. Reading s.n.*, Aug. 1982 (MO, photo DAO); wet rock polygons northeast of Bissett Lake, 63°49'45"N 95°24'08"W, *K.L. Reading s.n.*, August 1982 (MO, photo DAO); north of Bernier Lake, 61°21'08"N 98°25'10"W, *K.L. Reading s.n.*, 12 July 1992 (MO, photo DAO).

Porsild and Cody (1980) knew this species in the District of Keewatin from only two sites which were adjacent to longitude 100°W. The specimens cited above were from sites about 230 kilometers to the east.

Epilobium hornemannii Rchb. – MACKENZIE: mouth of Cameron River on Prosperous Lake NE of Yellowknife, 62°31'30"N 114°09'00"W (MO, photo DAO).

The specimen cited above is an extension of the known range of this rare species in the Territory of about 450 kilometers east of the Hot Springs area south of the Canada Tungsten Mine in the Mackenzie Mountains reported by Cody (1996).

Epilobium leptophyllum Raf. – MACKENZIE: Uplands Lake, 62°28'30"N 114°41'00"W, *K.L. Reading s.n.*, 10 Oct. 1981 (MO, photo DAO).

Porsild and Cody (1980) knew this rare species in the Territory only from adjacent to the Liard River. The specimen cited above is an extension of the known range in the Territory of about 450 kilometers to the east.

Epilobium palustre L., Swamp Willowherb – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'W, *K.L. Reading 33*, 10 Oct. 1998 (DAO); KEEWATIN: spruce bog, Snowdrift River (Stark River), 62°25'N 110°40'W, *K.L. Reading s.n.*, 25 Aug. 1988 (MO, photo DAO); stony pond margin, west of TK camp on Bissett Lake, 63°41'50"N 95°37'W, *K.L. Reading s.n.*, 24 July 1982 (MO, photo DAO).

The first specimen cited above is from a site about 120 kilometers south of the vicinity of Coppermine and about 80 kilometers east of a site at the east end of Great Bear Lake (Porsild and Cody 1980). The second specimen is from a site about 180 kilometers northeast and northwest of sites mapped by Porsild and Cody (1980). The third specimen is from a site about 250 kilometers east of a site mapped by Porsild and Cody (1980) west of longitude 100°W.

APIACEAE (UMBELLIFERAE)

Angelica lucida L. (*Coelopleurum gmelinii* (DC.) Ledeb.), Seacoast Angelica – MACKENZIE: mountain in Liard Range, NW of Fort Liard, 60°31'40"N 123°46'48"W, *Sharp et al. 3261*, 11 Aug. 1994 (DAO).

This Amphi-Beringian species was considered rare in the Northwest Territories (McJannet et al. 1995) on the basis of a specimen collected on Pointed Mountain, 60°22'N 123°55'W, (Cody 1978; Porsild and Cody 1980). The specimen cited above is only the second record for the Northwest Territories. In the Yukon Territory where it was also considered rare (Douglas et al. 1981) the known range of this species was recently extended to the La Biche River area in the extreme southeast (Cody et al. 1998).

Osmorhiza depauperata Phil. – MACKENZIE: Meilleur Hotspring (along the Meilleur River, a few km southwest of Deadmen Valley), 61°07'51"N 124°54'12"W, *J.M. Line, D. Tate and J. Doubt 2000-395*, 24 Aug. 2000 (DAO).

The specimen cited above is only the second known from the Territory (Porsild and Cody 1980). It was from a site about 130 kilometers northwest of a site adjacent to Mount Coty north of Fort Liard.

PYROLACEAE

Pyrola minor L. – KEEWATIN: south of east arm of Tyrell Arm of Yathkyed Lake area, 62°10'23"N 97°50'05"W, *K.L. Reading s.n.*, 19 July 1984 (DAO); radioactive site, east of Kazan Falls, 63°43'N 95°51'W, *K.L. Reading s.n.*, Aug. 1993 (DAO).

Porsild and Cody (1980) knew this taxon in the Continental District of Keewatin from a single locality in the extreme southwest. The first specimen cited above is just north of that one. The second specimen cited above is the northernmost yet found in this Territory, but it is known from the District of Mackenzie at this level just west of the Mackenzie/Keewatin border.

ERICACEAE

Chamaedaphne calyculata (L.) Moench, Leather-leaf – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'W, *K.L. Reading 3*, 15 Sept.-10 Oct. 1998 (DAO).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 120 kilometers northeast of a site adjacent to Port Radium at the east end of Great Bear Lake.

Ledum groenlandicum Oeder, Labrador-tea – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'W, *K.L. Reading 2*, 15 Sept.-10 Oct. 1998 (DAO).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 120 kilometers northeast of a site adjacent to Port Radium at the east end of Great Bear Lake.

Oxycoccus microcarpus Turcz., Bog Cranberry – KEEWATIN: South Yathkyed area, 62°17'00"N 97°42'00"W, *K.L. Reading s.n.*, 15 July 1984 (photo DAO).

Porsild and Cody (1980) knew this species in Continental District of Keewatin from only three sites in the southwest. The specimen cited above is the fourth known from that region.

Phyllodoce coerulea (L.) Bab. – KEEWATIN: south of east arm of Tyrell Arm of Yathkyed Lake, 62°14'08"N 97°51'30"W, *K.L. Reading s.n.*, 5 July 1984 (DAO).

Porsild and Cody (1980) knew this species from only four sites in Continental District of Keewatin in the southwest. The specimen cited above is from a site intermediate between sites previously mapped.

Phyllodoce empetriformis (Sm.) D. Don, Pink Mountain Heather – MACKENZIE: *Abies lasiocarpa* krummholz, Liard Range, Mackenzie Mountains, 60°34'N 123°46'W, *R. Mueller LR-20-2*, 12 Aug. 1994 (DAO).

This species was not included in the *Rare Vascular Plants in the Northwest Territories* (McJannet et al. 1995) because it has a widespread cordilleran distribution. The specimen cited above is a southward extension of the known distribution in the Mackenzie Mountains of about 75 kilometers from a site in Nahanni National Park (Porsild and Cody 1980).

Vaccinium ovalifolium J.E. Smith, Oval-leaved Blueberry – MACKENZIE: *Abies lasiocarpa*-feathermoss forest, Liard Range, Mackenzie Mountains, 60°34'N 123°46'W, *R. Mueller LR-18-1*, 12 Aug. 1994 (DAO).

This species is new to the flora of the Northwest Territories and should be added to the list of rare plants in the region (McJannet et al. 1995). It is also rare in the Yukon Territory (Douglas et al 1981) although additional collections have been recorded (Cody, Kennedy, and Bennett 1998, 2000), including one in the extreme southeast from

Beavercrow Ridge at 60°14'N 124°32'W adjacent to the specimen cited above.

PRIMULACEAE

Primula incana M.E. Jones, Mealy Primrose – MACKENZIE: hummocks, Walker Bay, Kent Peninsula, 68°21'N 108°06'W, *G. Loh 21*, 16 July 1996 (DAO); island in Anderson River, Reindeer Grazing Preserve, 68°33'N 128°28'W, *G.W. Scotter 7294*, 5 July 1965 (DAO); rare, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 33-1*, 23 July 1995 (DAO).

Porsild and Cody (1980) mapped this species as far north as the vicinity of Norman Wells in the Mackenzie River Valley. The specimens cited above extends the known range in the Northwest Territories northward some 500 kilometers to the Anderson River and northeastward some 550 kilometers to the Kent Peninsula.

GENTIANACEAE

Gentianella propinqua (Richards.) J.M. Gillett ssp. *propinqua* (*Gentiana propinqua* Richards.) – MACKENZIE: locally common, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 30-1*, 22 July 1999 (DAO).

The specimen cited above is from a site about 120 kilometers south of Coppermine and about 90 kilometers northeast of a site adjacent to the southeastern bay of Great Bear Lake (Porsild and Cody 1980).

Halenia deflexa (Sm.) Griseb., Spurred Gentian – MACKENZIE: occasional on thin peat over mineral soil, moist places, seismic line NE of Barefoot Lake, SE of Trout Lake, 60°20'N 120°45'W, *J.S. Rowe 1779*, 8 July 1971 (DAO).

The specimen cited above which is a new record for the Northwest Territories, is an extension from the known range in Alberta (Packer 1983) of about 650 kilometers northwest of a site adjacent to the Athabasca River in the vicinity of Forks Fort. *Halenia deflexa* should be added to the *Rare Vascular Plants in the Northwest Territories* (McJannet et al. 1995).

This is an annual herb with a taproot; stems erect, solitary, simple or branched above, 10-50 cm tall. Basal leaves oblanceolate or spatulate, petioled; cauline leaves lanceolate to ovate, 2-4 cm long, sessile or subsessile. Flowers in terminal or axillary cymes; calyx deeply 4-cleft, the lobes lanceolate, acuminate; corolla purplish green or bronze, with a short tube, 4-lobed usually prolonged at the base into a slender spur; stamens 4; stigmas 2. It is found in North America from Newfoundland to eastern British Columbia south into the United States.

A. Corolla, at least in the larger flowers, 4-spurred at the base ..... *Halenia*
A. Corolla not spurred at the base ..... *Gentiana* and ..... *Gentianella*

Lomatogonium rotatum (L.) Fries ssp. *rotatum*, Marsh Felwort – MACKENZIE: mudflats, Walker Bay, Kent Peninsula, 68°21'N 108°06'W, *D. Wilson 3*, 11 July 1996 (DAO).

The specimen cited above is the most northeasterly collection yet found in the District of Mackenzie. The nearest previously known site was about 160 kilometers to the south near the foot of Bathurst Inlet (Porsild and Cody 1980).

MENYANTHACEAE

Menyanthes trifoliata L., Buckbean – KEEWATIN: south of east arm of Tyrell Arm of Yathkyed Lake, 62°22'30"N 97°23'00"W, *K.L. Reading s.n.*, 17 Aug. 1984 (DAO).

Porsild and Cody (1980) knew this species from only two localities in Continental District of Keewatin. The specimen cited above is from an intermediate site.

APOCYNACEAE

Apocynum cannabinum L. var. *glaberrimum* A.DC. (*A. sibiricum* Jacq.), Common Dogbane – MACKENZIE: *Populus balsamifera* regeneration on Muskeg River shoreline, 60°10'N 123°18'W, *R. Mueller FTL-13-10*, 4 Aug. 1994 (DAO); north side roadbank, Willowlake River winter road, 500 m west of Norman Wells Pipeline Km 380, 62°43'N 123°05'W, *K.L. MacInnes 86-93*, 16 July 1986 (DAO).

This species was included in the *Rare Vascular Plants in the Northwest Territories* (McJannet et al. 1995) on the basis of two collections: West Channel, Hay River and opposite Fort Simpson. The Muskeg River site is about 200 kilometers southwest of Fort Simpson and the Willowlake River is about 145 kilometers north of Fort Simpson (Porsild and Cody 1980).

POLEMONIACEAE

Polemonium boreale Adams, Northern Jacob's-ladder – MACKENZIE: lichen-moss herbmat, Liard Range, Mackenzie Mountains, *G. Brunner LR-5-6*, 11 Aug. 1994 (DAO).

This species was not included in the *Rare Vascular Plants in the Northwest Territories* (McJannet et al. 1995) because it has a widespread Amphi-Beringian distribution. The specimen cited above is an extension of the known range in the Mackenzie Mountains about 150 kilometers south of latitude 63°N (Porsild and Cody 1980).

Polemonium boreale Adams forma *albiflorum* Cody forma nova, a forma typica differt corollis albis – MACKENZIE: on a sandy portion of a gravel bar, Horton River, 69°42'N 126°56'W, elev. 30 m, *G.W. Scotter 101016b*, 6 July 1995 (HOLOTYPE DAO); YUKON: fox den, Herschel Island, 69°30'N 139°15'W, *C.E. Kennedy 262*, 16 July 1985 (DAO).

At the Horton River site this white flowered form, which has a yellow tube, was growing beside the typical purplish-blue form which also has a yellow tube.

BORAGINACEAE

Mertensia drummondii (Lehm.) G. Don, Drummond's Lungwort – MACKENZIE: gravel bar near the river, Horton River, 69°24'N 126°50'W, *G.W. Scotter 101011*, 3 July 1995 (DAO).

Cody et al. (1992) extended the known range of this Arctic Coast endemic 80 kilometers westward from Cape Young to the Crocker River Delta (119°07'W). McJannet et al. (1995) mapped specimens collected by Scotter and

Zoltai at 124°25'W and 124°39'W, a further extension westward of some 215 kilometers. The specimen cited above extends the known range in the District of Mackenzie further westward some 85 kilometers.

LAMIACEAE (LABIATAE)

Lycopus uniflorus Michx., Northern Water Horehound – MACKENZIE: *Equisetum* and *Carex* marsh in old river channel dammed by beavers, south bank of Liard River, NE of Ft. Liard, 60°43'10"N 123°24'34"W, *Kubiw et al. 1031*, 15 Aug. 1994 (DAO).

This species was considered rare in Northwest Territories (Porsild and Cody 1980; McJannet et al. 1995) based on two collections in the Precambrian Shield area south of Great Slave Lake. The specimen cited above is an extension of the known range in the Territory of about 700 kilometers to the west.

SCROPHULARIACEAE

Pedicularis flammea L. – KEEWATIN: east of Bernier Lake, 61°23'46"N 98°20'00"W, *K.L. Reading s.n.*, 6 July 1992 (DAO).

Porsild and Cody (1980) knew this taxon in the Continental District of Keewatin from only five sites in the southeast. The specimen cited above is the westernmost yet found in the Territory.

Pedicularis lanata Cham. and Schlecht., Woolly Lousewort – KEEWATIN: west of Henick Lake, 61°26'00"N 97°55'46"W, *K.L. Reading s.n.*, 18 July 1992 (DAO).

Porsild and Cody (1980) knew this taxon from only three sites in the Continental District of Keewatin. The specimen cited above is the southernmost yet found in this Territory.

Pedicularis macrodonta Richards. (*P. parviflora* sensu Porsild and Cody 1980) – MACKENZIE: common in wet fen hollows between *Sphagnum* hummocks near Tetcho Lake, SE of Trout Lake, 60°25'N 120°45'W, *J.S. Rowe s.n.*, 9 July 1971 (DAO).

This species was considered rare in the Continental Northwest Territories (Porsild and Cody 1980; McJannet et al. 1995) based on two collectins: KEEWATIN, mouth of McConnell River, 60°50'N 94°25'W, *K.L. MacInnes 89*, 13 July 1964 (DAO) and MACKENZIE, S. Heart Lake, 60°50'N 116°39'W, *S.S. Talbot 3702*, 27 July 1972 (DAO). The specimen cited above is from a site about 885 kilometers west of the S. Heart Lake site.

CAPRIFOLIACEAE

Linnaea borealis L. var. *americana* (Forbes) Rehd., Twinflower – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'W, *K.L. Reading 17*, 15 Sept.–10 Oct. 1998 (DAO).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 80 kilometers east of sites adjacent to the east side of Great Bear Lake.

ADOXACEAE

Adoxa moschatellina L., Moschatel – MACKENZIE: beside a cool creek in dark conifer woods near hotsprings, Hole-in-the-Wall Lake, 61°46'23"N 127°18'04"W, *J.M. Line 2000-352*, 22 Aug. 2000 (DAO).

This is a rare species in the Northwest Territories (McJannet et al. 1995). It was first reported from the lower Liard River by Jeffrey (1961). Sheila Lamont collected it in 1973 and again in 1974 at Fisherman Lake northwest of Fort Liard (specimens in DAO). The specimen cited above is an extension of the known range in the Territory of about 275 kilometers northwest of Fisherman Lake.

LOBELIACEAE

Lobelia dortmanna L., Water Lobelia – MACKENZIE: Cameron River, about 50 miles northeast of Yellowknife, *K.L. Reading s.n.*, 17 Aug. 1995 (DAO).

This species was first reported in the District of Mackenzie by Cody (1979) from southwest of Abitau Lake, 60°22'N 107°19'W, where it was found in shallow water. The specimen cited above is an extension of the known range in the Territory of about 450 kilometers to the northwest.

ASTERACEAE (COMPOSITAE)

Artemisia campestris L. s.l., *A. borealis* Pall., Northern Wormwood – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'W, *K.L. Reading 30*, 10 Oct. 1998 (DAO).

The specimen cited above is from a site about 80 kilometers east of a site adjacent to Great Bear Lake (Porsild and Cody 1980).

Artemisia tilesii Ledeb., Aleutian Mugwort – MACKENZIE: Big Bend Area, Coppermine River, 66°52'38"N 115°50'W, *K.L. Reading 31*, 10 Oct. 1998 (DAO).

The specimen cited above is from a site about 120 kilometers south of the vicinity of Coppermine and 80 kilometers east of a site adjacent to eastern Great Bear Lake (Porsild and Cody 1980).

Aster sibiricus L., Arctic Aster – MACKENZIE: Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 21-1*, 11 July 1999 (DAO); same locality, *K.L. Reading 34-1*, 20 Aug. 1999 (DAO) and *K.L. Reading 15*, 10 Oct. 1998 (DAO).

The specimens cited above are from an area about 120 kilometers south of Coppermine and 80 kilometers east of the eastern bay of Great Bear Lake (Porsild and Cody 1980).

Aster spathulatus Lindl., Aster – MACKENZIE: Balsam poplar-*Alnus* riparian terrace community at junction of creek and Liard R., off Liard Hwy., NE of Ft. Liard, 60°45'5"N 123°18'56"W, *Kubiw and Cowell 1039*, 14 Aug. 1994 (DAO).

Porsild and Cody (1980) mapped this endemic species from the Mackenzie River Valley between Fort Simpson and the Great Bear River and at the eastern and western ends of Great Bear Lake. The specimen cited above extends the known range about 300 kilometers to the south to the Liard River Valley just north of the British Columbia border.

Chrysanthemum integrifolium Richards., Entire-leaved Daisy – MACKENZIE: common, Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 9-1*, 7 July 1999 (DAO); same locality, *K.L. Reading 24*, 10 Oct. 1998 (DAO).

The specimens cited above are the southernmost yet found in the Coppermine River system. The nearest site is about half way between Big Bend and Coppermine (Porsild and Cody 1980).

Crepis tectorum L., Annual Hawk's-beard – MACKENZIE: tall willow shrub-riparian bar, Liard River, south of Ft. Liard, 60°03'32"N 123°49'37"W, *Kubiw et al. 1028*, 17 Aug. 1994 (DAO).

Porsild and Cody (1980) knew this introduced species in the vicinities of Fort Smith and the Yellowknife and Mackenzie highways. It is now also common adjacent to the Norman Wells Pipeline (Cody, MacInness, Cayouette, and Darbyshire 2000). The specimen cited above is the first known from the Liard River area.

Petasites frigidus (L.) Fries ssp. *palmatus* (Ait.) Cody (*P. palmatus* (Ait) Gray), Sweet Coltsfoot – KEEWATIN: northwest corner of Mountain Lake, 61°13'05"N 98°37'35"W, *K.L. Reading s.n.*, 14 June 1991 (DAO).

Porsild and Cody (1980) knew this taxon from only two localities in the extreme south of the Continental District of Keewatin. The specimen cited above is a slight extension of the known range in the Territory to the north.

Petasites sagitatus (Banks ex Pursh) Gray, Arrow-leaved Coltsfoot – KEEWATIN: east of Mountain Lake, 61°12'18"N 98°31'20"W, *K.L. Reading s.n.*, 16 June 1991 (DAO); Big Bird Lake, 62°17'06"N 97°37'25"W, *K.L. Reading s.n.*, 29 June 1985 (DAO); south of east arm of Tyrell Arm of Yathkyed Lake, 62°12'00"N 97°50'35"W, *K.L. Reading s.n.*, 5 July 1984 (DAO).

Porsild and Cody (1980) knew this taxon from a single collection in the extreme south of the Continental District of Keewatin. The specimens cited above were collected in the same region as mapped by Porsild and Cody.

Taraxacum lyratum (Ledeb.) DC. (*T. phymatocarpum* J. Vahl) – MACKENZIE: Big Bend Area, Coppermine River, approx. 66°52'N 115°50'W, *K.L. Reading 25-1*, 14 July 1999 (DAO).

The specimen cited above is an extension of the known range in the Territory (Porsild and Cody 1980) of about 120 kilometers south of the vicinity of Coppermine.

Acknowledgements

We thank the many individuals who have contributed specimens to the DAO Herbarium; George Argus for the identification of *Salix* specimens; Stephen Darbyshire for the identification of *Vahlodea atropurpurea*; Harold C. Hinds for the identification of *Polygonum hudsonianum*; Gerald A. Mulligan for the identification of Brassicaceae (Cruciferae) specimens; John McNeill for the identification of *Polygonum fowleri* and *P. ramosissimum*; Anton A. Reznick for the identification for *Carex* specimens; Ernest Small for the identification of *Medicago sativa* ssp. *falcata*; John K. Morton for the identification of *Silene uralensis*; and especially Leslie Durocher, for the many hours inputting this information on her computer. Jennifer Line also thanks Doug Tate and other staff at Nahanni National Park Reserve for the opportunity to conduct surveys in the park. We all thank Paul Catling for reviewing an earlier version of this manuscript.

Literature Cited

Cody, W. J. 1954. A history of *Tillaea aquatica* (Cressulaceae) in Canada and Alaska. Rhodora 56: 96-101.

Cody, W. J. 1956. New plant records for northern Alberta and southern Mackenzie District, N.W.T. Canadian Field-Naturalist 70: 101-130.

Cody, W. J. 1978. Range extensions and comments on the vascular flora of the continental Northwest Territories. Canadian Field-Naturalist 92: 144-150.

Cody, W. J. 1979. Vascular plants of restricted range in the continental Northwest Territories, Canada. Syllogeus 23, National Museum of Natural Sciences, Ottawa. 57 pages.

Cody, W. J. 1996. Additions and range extensions to the vascular plant flora of the Northwest Territories, Canada. Canadian Field-Naturalist 110: 260-270.

Cody, W. J. 1996. Flora of the Yukon Territory. National Research Council (NRC) Press, Ottawa, Ontario, Canada. 643 pages.

Cody, W. J. 1998. Horned Pondweed, *Zannichellia palustris* (Zannichelliaceae), new to the vascular plant flora of the continental Northwest Territories, Canada, and deleted from the flora of the Yukon Territory. Canadian Field-Naturalist 112: 711-712.

Cody, W. J., and **D. M. Britton**. 1989. Ferns and fern allies of Canada. Agriculture, Research Branch, Publication 1818/E. 320 pages.

Cody, W. J., and **V. Johnston**. 2003. *Malaxis monophyllos* var. *brachypoda* one-leaved *Malaxis*, new to the Northwest Territories. Canadian Field-Naturalist 117: 302-303.

Cody, W. J., C. E. Kennedy, and **B. Bennett**. 1998. New records of vascular plants in the Yukon. Canadian Field-Naturalist 112: 289-328.

Cody, W. J., C. E. Kennedy, and **B. Bennett**. 2000. New records of vascular plants in the Yukon Territory II. Canadian Field-Naturalist 114: 417-443.

Cody, W. J., C. E. Kennedy, and **B. Bennett**. 2001. New records of vascular plants in the Yukon Territory III. Canadian Field-Naturalist 115: 301-322.

Cody, W. J., C. E. Kennedy, B. Bennett, and **V. Loewen**. 2002. New records of vascular plants in the Yukon Territory IV. Canadian Field-Naturalist 116: 446–474.

Cody, W. J., K. L. MacInness, J. Cayouette, and **S. Darbyshire**. 2000. Alien and invasive native vascular plants along the Norman Wells Pipeline, District of Mackenzie, Northwest Territories. Canadian Field-Naturalist 114: 126-137.

Cody, W. J., G. W. Scotter, and **S. S. Talbot**. 1979. Additions to the vascular plant flora of Nahanni National Park, Northwest Territories. Le Naturaliste canadien 106: 439-450.

Cody, W. J., G. W. Scotter, and **S. C. Zoltai**. 1984. Additions to the vascular plant flora of Bathurst Inlet, Northwest Territories, Canada. Canadian Field-Naturalist 98: 171-177.

Cody, W. J., G. W. Scotter, and **S. C. Zoltai**. 1989. Vascular plant flora of the Wager Bay Region, District of Keewatin, Northwest Territories. Canadian Field-Naturalist 103: 551-559.

Cody, W. J., G. W. Scotter, and **S. C. Zoltai**. 1992. Vascular plant flora of the Melville Hills Region, Northwest Territories. Canadian Field-Naturalist 106: 87-99.

Cody, W. J., and **S. S. Talbot**. 1978. Vascular plant range extensions to the Heart Lake Area, District of Mackenzie, Northwest Territories. Canadian Field-Naturalist 92: 137-143.

Douglas, G. W., G. W. Argus, H. L. Dickson, and **D. F. Brunton**. 1981. The rare vascular plants of the Yukon. Syllogeus (28), Canadian Museum of Nature, Ottawa. 96 pages.

Jeffrey, W. W. 1961. Notes on plant occurrence along lower Liard River, N.W.T. National Museum of Canada Bulletin (171): 32-115.

McJannet, C. L., G. W. Argus, and **W. J. Cody**. 1995. Rare vascular plants in the Northwest Territories. Syllogeus (73), Canadian Museum of Nature, Ottawa. 104 pages.

Mosyakin, S. L. 1995. New taxa of *Corispermum* L. (Chenopodiaceae) with preliminary comments on the taxonomy of the genus in North America. Novon 5: 340-353.

Packer, J. G. 1983. Flora of Alberta. Second Edition, University of Toronto Press, Toronto, Ontario. 687 pages.

Porsild, A. E. 1943. Materials for a flora of the continental Northwest Territories of Canada. Sargentia 4: 1-79.

Porsild, A. E., and **W. J. Cody**. 1980. Vascular plants of continental Northwest Territories, Canada. National Museum of Natural Sciences, Ottawa. 667 pages.

Scotter, G. W. 1966. A contribution to the flora of the Eastern Arm of Great Slave Lake, Northwest Territories. Canadian Field-Naturalist 80: 1-18.

Scotter, G. W., and **W. J. Cody**. 1974. Vascular plants of Nahanni National Park and vicinity, Northwest Territories. Naturalist Canadien 101: 861-891.

Timoney, K. P. 2001. String and net-patterned salt marshes: rare landscape elements of boreal Canada. Canadian Field-Naturalist 115: 406-412.

Wein, R. W., G. Wein, S. Bahret, and **W. J. Cody**. 1992. Invading plant species in and adjacent to Wood Buffalo National Park, Canada. Canadian Field-Naturalist 106: 216-224.

Received 9 October 2002
Accepted 11 August 2003

Notes

Black Color Morph of the Brown Lemming, *Lemmus trimucronatus* = *L. sibiricus*

DENVER W. HOLT[1], MICHAEL T. MAPLES[1], AND CHRIS SAVOK[2]

[1]Owl Research Institute, P.O. Box 39, Charlo, Montana 59824 USA; E-mail: owlmontana@charlo.net
[2]P.O. Box 2097, Barrow, Alaska 99723 USA

Holt, Denver W., Michael T. Maples, and Chris Savok. 2003. "Black" color morph of the Brown Lemming, *Lemmus trimuero-natus* = *L. sibiricus*. Canadian Field-Naturalist 117 (3): 466-468.

A black pelage Brown Lemming is reported from Barrow, Alaska. The occurrence of this black color morph appears to be rare. During twelve years of Snowy Owl research and lemming trapping, only one has been seen. Of 554 snap-trapped Brown Lemmings and 1649 Brown Lemmings found cached at owl nests, no black individuals were found. The pelage of the black morph is described using a Munsell Soil Color Chart.

Key Words: Brown Lemming, *Lemmus trimucronatus* = *L. sibiricus*, melanism, black morph, Alaska

Pelage coloration in lemmings can be more variable than other species of arvicoline rodents, particularly *Lemmus* and *Dicrostonyx* (Stenseth and Ims 1993). Pelage coloration in the Brown Lemming (*Lemmus trimucronatus* = *L. sibiricus*) can range through many phases from juvenile to adult growth, and can vary seasonally after subsequent molts. Basically, however, the overall color is brown with various intensities of yellow, red and black (Bee and Hall 1956). These colors likely reflect differences in the width and color of the subapical bands on individual hairs, similar to *Microtus* (see Gaines 1985). Polymorphism has not been reported for the Brown Lemming; however, albino and melanistic individuals are known (Bee and Hall 1956). Unfortunately, little accompanying information has been provided in the primary literature regarding these aberrant phenotypes (Bee and Hall 1956; Rausch and Rausch 1974; Stenseth and Ims 1993). The purpose of this paper is to describe the pelage coloration of a single "black" Brown Lemming using a standardized method, and to report the frequency of occurrence of this phenotype, relative to normally colored Brown Lemmings encountered in our study.

Study Area and Methods

DWH has studied Snowy Owls (*Nyctea scandiaca*) at Barrow, Alaska (71° 18' N, 156° 40' W) since 1992. During the course of study, researchers have snap-trapped small mammals (1992-2003), recorded prey cached at Snowy Owl nests (1993, 1995, 1996, 1999, 2000, 2002, 2003) and collected Snowy Owl pellets (1992-2003). Because owls have weak digestive enzymes (low acidity) (Duke et al. 1976), the regurgitated bone, hair, feathers and teeth of prey are reliable indicators of species eaten (Marti 1987; Holt et al. 1987). The color of pellets also reflects the pelage or plumage color of prey (Holt 1990). For example, blond colored pellets regurgitated by Short-eared Owls (*Asio flammeus*) were representative of "blond" morph Meadow Voles (*Microtus pennsylvanicus*) (Holt 1990).

Colors of small mammals are sometimes described using standardized color charts such as the Munsell Soil Color Chart system (see Holt 1990). These charts may be useful because they allow researchers to make standardized color comparisons over wide geographic areas. In this note, we used the Munsell Soil Color Chart (Munsell 2000) to score an aberrantly colored Brown Lemming.

Results

On 18 July 1995 MTM and CS observed a black Brown Lemming on the tundra, 1 km west of the airport at Barrow, Alaska (71° 16' N, 156° 44' W), while monitoring a Snowy Owl nest. The lemming was collected, photographed, described, weighed, sexed, reproductive status determined, and prepared as a study skin by MTM. The specimen was placed in the local Ilisaġvik College Natural History Museum, Barrow, Alaska. Currently, it has not been given an accession number. The lemming was entirely black dorsally, with few dark brown hairs on the tail tip (Figure 1). The dorsal and ventral colors were scored from the Munsell Soil Color Chart 1 (i.e., GLEY 1). Its Munsell color score was N 2.5/ and described as "black" dorsally, and N 3/ "very dark gray" ventrally. The speci-

FIGURE 1. Comparison of the "black" (right) and typically colored Brown Lemming.

men was a 101 g female with 3 and 4 embryos in the right and left uterine horns, respectively.

During the twelve years of study, researchers have snap-trapped 554 Brown Lemmings and counted 1649 Brown Lemmings cached at Snowy Owl nests. Of these 2203 Brown Lemmings, none were black. Researchers have also recorded the remains of over 31000 Brown Lemmings from about 8500 Snowy Owl pellets, and have not detected any pellets composed of black fur, although some could have been overlooked. Furthermore, during these twelve years of study, 19 owl researchers have hiked the tundra within our 213 km^2 study area almost daily from mid-June to 01 September, logging hundreds of kilometres individually and annually – and yet, this is the only observation of a black Brown Lemming.

Discussion

The occurrence of black Brown Lemmings has generally been reported in the literature; however, specific details concerning numbers, location and relative frequency of occurrence are lacking (Bee and Hall 1956; Rausch and Rausch 1974; R. Rausch, personal communication). Rausch and Rausch (1974) mentioned that "a small proportion of melanistic brown lemmings were present in the vicinity of Barrow in 1953", but gave no details. A few of these "melanistic" individuals were captured alive and later bred in captivity at the Arctic Health Research Center in Fairbanks (AHRC), (R. L. Rausch, personal communication). This breeding colony was maintained from 1954 to 1958 when it was "lost", then restarted in 1959, once again with Brown Lemmings from Barrow, and continued to 1974 (Rausch and Rausch 1974). Other captive Brown Lemming colonies also existed at this time in Barrow and Anchorage, Alaska (Thompson 1955a; Thompson 1955b; R. L. Rausch, personal communication). Rausch and Rausch (1974) determined that a recessive gene was responsible for the melanistic color morph.

Because specific information regarding black morph Brown Lemmings was not provided in the primary literature, we checked the vertebrate collection at the University of Alaska Museum, Fairbanks, to determine if black Brown Lemmings had been recorded from Barrow. Surprisingly, 12 specimens existed: 5 males and 7 females. All were reported to have come from or were thought to have come from Barrow, between 1959 and 1964. All specimen labels indicated the lemmings were collected by Harry K. Brower or Otto W. Geist.

The specimen labels indicated that seven of these were captives from Barrow, two others were found in Barrow but with no specific data, two more are not known if found in Barrow, and only one was reported to have come form the tundra near Barrow. No other details were provided. Thus, given the high proportion of melanistic individuals in such a short time period (1959 to 1964) and the fact that little or no field data exist on the specimen tags, it is conceivable that most of these 12 individuals were bred in captivity (R. Rausch, personal communication). This confusion reiterates the need for recording specific details of aberrant individuals. No other museums were checked.

Several studies have examined the role of pelage color variation in small mammals and most conclude that predation may be the selective force driving pelage color (crypsis), which tends to match the background of the habitats occupied (Belk and Smith 1996; Krupa and Geluso 2000). Cryptic and aposematic coloration however, may both act in the Norwegian Lemming (*Lemmus lemmus*) (Taitt 1993). Whether this black phenotype exerts any selective advantage or disadvantage or is just an aberrant mutation is currently unknown. However, we reasonably conclude the black color morph is exceedingly rare.

Aberrant color morphs should be reported however, their color variation should be described in a standard and replicable manner (i.e., color charts). These standards should then reduce confusion when describing new color morphs. Furthermore, exact locality and detailed notes of aberrant morphs should be taken to help determine distribution and if the morph is localized or not.

Acknowledgments

Robert Rausch provided helpful comments on drafts of the manuscript. Gorden Jarrell provided museum data. Mark Korti, Amie Stevens, Lara Dehn helped in many ways in the field and lab. Daniel J. Cox, Natural Exposures, Bozeman, Montana, took the photo. We thank them all.

Literature Cited

Bee, J. W., and **E. R. Hall.** 1956. Mammals of Northern Alaska. Miscellaneous Publication (8): 1-309, University of Kansas Museum of Natural History, Lawrence, Kansas.

Belk, M. C., and **M. H. Smith.** 1996. Pelage coloration in Oldfield Mice (*Peromyscus polionotus*): antipredator adaptation. Journal of Mammalogy 77: 882-890.

Duke, G. E., O. A. Evanson, and **A. Jegers.** 1976. Meal to pellet intervals in 14 species of captive raptors. Comparative Biochemistry and Physiology 53: 1-6.

Gaines, M. S. 1985. Genetics. Pages 845-883 *in* Biology of New World *Microtus*. *Edited by* R. H. Tamarin. Special Publication (8): 1-893, American Society of Mammalogists.

Holt, D.W. 1990. "Blond" color morph of Meadow Voles, *Microtus pennsylvanicus*, from Massachusetts. Canadian Field-Naturalist 104: 596-597.

Holt, D. W., L. J. Lyons, and **R. Hale.** 1987. Techniques for differentiating the pellets of Short-eared Owls and Northern Harriers. Condor 89: 929-931.

Krupa, J. J., and **K. N. Geluso.** 2000. Matching the color of excavated soil: cryptic coloration in the Plains Pocket Gopher (*Geomys bursarius*). Journal of Mammalogy 81: 86-96.

Marti, C. D. 1987. Raptor food habits studies. Pages 67-80 *in* Raptor Management Techniques Manual. *Edited by* B. A. Giron-Pendleton, B. A. Millsap, K. W. Kline and D. M. Bird. Technical Series (10). National Wildlife Federation, Washington, D.C.

Munsell Soil Color Charts. 2000. Gregtag/MacBeth, New York.

Rausch, R. L., and **V. R. Rausch.** 1974. Taxonomy and zoogeography of *Lemmus* spp. (Rodentia: Arvicolinae), with notes on laboratory-reared lemmings. Zeitschrift fur Saugetierkunde 40: 8-34.

Stenseth, N. C., and **R. A. Ims.** 1993. The evolutionary history and distribution of lemmings – an introduction. Pages 37-43 *in* The Biology of Lemmings. *Edited by* N. C. Stenseth and R. A. Ims. Academic Press, London.

Taitt, M. J. 1993. Adaptive coloration in *Lemmus lemmus*: Why aren't Norwegian Lemmings brown? Pages 439-445 *in* The Biology of Lemmings. *Edited by* N. C. Stenseth and R. A. Ims. Academic Press, London.

Thompson, D. Q. 1955a. The ecology and population dynamics of the Brown Lemming (*Lemmus trimucronatus*) at Point Barrow, Alaska. Unpublished Ph.D. Dissertation, University of Missouri, Columbia. 138 pages.

Thompson, D. Q. 1955b. The 1953 lemming emigration at Point Barrow, Alaska. Arctic 8: 37-45.

Received 6 March 2001
Accepted 9 February 2004

White Color Phase of the Swift Fox, *Vulpes velox*

JAN F. KAMLER[1] and WARREN B. BALLARD

Department of Range, Wildlife, and Fisheries Management, Box 42125, Texas Tech University, Lubbock, Texas 79409 USA
[1]Present address: Polish Academy of Sciences, Mammal Research Institute, 17-230 Biatowieża, Poland

Kamler, Jan F., and Warren B. Ballard. 2003. White color phase of the Swift Fox, *Vulpes velox*. Canadian Field-Naturalist 117(3): 468-469.

While live-trapping Swift Foxes (*Vulpes velox*) in northwestern Texas, we captured and radio-collared a Swift Fox that exhibited a white pelage and light blue eyes. Although white color phases and light blue eyes have been reported for other canid species, this is the first documentation for Swift Foxes.

Key Words: Swift Fox, *Vulpes velox*, Texas, white color phase.

Although Gray Wolves (*Canis lupus*) and Red Foxes (*Vulpes vulpes*) can exhibit several color phases (Ballard and Gipson 2000; Kamler and Ballard 2002), most canid species, including Coyotes (*Canis latrans*), Gray Foxes (*Urocyon cinereoargenteus*), Kit Foxes (*Vulpes macrotis*), and Swift Foxes (*Vulpes velox*), exhibit only one color phase. Variations in eye color are rarely reported for any canid species. We document the occurrence of a white color phase and light blue eyes in the Swift Fox.

On 26 September 2000, at Rita Blanca National Grasslands (36-2° N, 102-40° W) in Dallam County, Texas, we captured and radio-collared a juvenile female Swift Fox that had a white pelage and light blue eyes (trapping was part of a research project on Swift Fox ecology in Texas). We recaptured this individual six times and monitored her on the study site until late December when she presumably dispersed. This individual was not an albino since the eyes were light blue rather than pink, and some guard hairs on the tail, back, and muzzle were black. Photographs of the white Swift Fox are deposited in The Museum, Texas Tech University, Lubbock.

We interviewed a local trapper (with no knowledge of the white Swift Fox we captured) who stated he captured a juvenile male and an adult male Swift Fox with white pelage and light blue eyes in January 2001 on land adjacent to our study area. This man also stated that he trapped Swift Foxes in that area for approximately 20 years, but had never previously captured

white Swift Foxes. This information suggests that the white color phase and light blue eyes are a genetic mutation that can be inherited by Swift Foxes.

A white pelage and/or light blue eyes have been reported in other canid species. In addition to albino Coyotes documented by Young and Jackson (1951), one litter of Coyotes in Nebraska contained four young that had a white pelage and milky blue eyes, suggesting those characteristics were inherited. Cole and Shackleford (1943) reported that some litters of farm-raised Red Foxes contained all white pups. Gray Wolves exhibit a white color phase, especially in the high Arctic (Miller 1995), and light blue eyes also have been reported in this species (Mech 2000).

Acknowledgments

This research project was funded by Texas Tech University and Texas Parks and Wildlife Department. This is Texas Tech University College of Agricultural Sciences and Natural Resources technical publication T-9-899.

Literature Cited

Ballard, W. B., and **P. S. Gipson.** 2000. Wolf. Pages 321-346 *in* Ecology and management of large mammals in North America. *Edited by* S. Demarais and P. R. Krausman. Prentice-Hall, Inc., Upper Saddle River, New Jersey.

Cole, L. J., and **R. M. Shackleford.** 1943. White spotting in the fox. American Naturalist 77: 289-321.

Kamler, J. F., and **W. B. Ballard.** 2002. A review of native and nonnative red foxes in North America. Wildlife Society Bulletin 30: 370-379.

Mech, L. D. 2000. The wolves of Minnesota: howl in the heartland. Voyageur Press, Stillwater, Minnesota. 128 pages.

Miller, F. L. 1995. Status of wolves on the Canadian arctic islands. Pages 35-42 *in* Ecology and conservation of wolves in a changing world. *Edited by* L. N. Carbyn, S. H. Fritts, and D. R. Seip. Canadian Circumpolar Institute, Edmonton, Alberta.

Young, S. P., and **H. T. Jackson.** 1951. The clever coyote. University of Nebraska Press, Lincoln. 411 pages.

Received 16 May 2001
Accepted 22 March 2004

Death of Gray Wolves, *Canis lupus,* in Porcupine, *Erethizon dorsatum*, Dens in Wisconsin

ADRIAN P. WYDEVEN[1], SARAH R. BOLES[1], RONALD N. SCHULTZ[1], and C. J. THOMAS DOOLITTLE[2]

[1]Wisconsin Department of Natural Resources, 875 S. 4th Ave., Park Falls, Wisconsin 54552 USA
[2]Bad River Band of Chippewa, Environmental Protection/Natural Resource Department, Odanah, Wisconsin 54861 USA

Wydeven, Adrian P., Sarah R. Boles, Ronald N. Schultz, and Thomas C. J. Doolittle. 2003. Death of Gray Wolves, *Canis lupus*, in Porcupine, *Erethizon dorsatum*, dens in Wisconsin. Canadian Field-Naturalist 117(3): 469-471.

Three Gray Wolves (*Canis lupus*) were found dead in porcupine (*Erethizon dorsatum*) dens in northern Wisconsin between 1996-2000. Use of these dens appeared to be cases of shelter-seeking behavior by wolves suffering from sarcoptic mange.

Key Words: Gray Wolf, *Canis lupus,* Porcupine, *Erethizon dorsatum,* den, sarcoptic mange.

Mammals suffering the affects of debilitating diseases may display unusual behavior in attempts to alleviate discomfort. Gray Wolves (*Canis lupus*) affected by sarcoptic mange may lose normal fears and attempt to seek shelter in areas not normally used by them, including buildings (Todd et al. 1981). During a 35-day period in December 1995-January 1996, four of 25 radio-collared wolves being monitored, including wolf 234M, died with severe mange cases (Wisconsin DNR files). One of the mange affected wolves had also been shot, while effects of sarcoptic mange was the primary cause of death of the other three. We describe one of these wolves with mange seeking shelter and dying in Porcupine (*Erethizon dorsatum*) den in Wisconsin, and describe two additional wolves that died in Porcupine dens in later years.

Wolf populations in Wisconsin have been monitored annually since 1979 by snowtrack surveys, and by livecapturing and radiotracking (Wydeven et al. 1995). On 10 January 1996, a mortality signal was received from adult 234M, a male collared initially 14 May 1994, that appeared to have been living as a loner at the periphery of the Torch River Pack since summer 1996.

Wolf 234M was located in a porcupine den at the base of an uprooted Red Maple (*Acer rubrum*) with an opening height of 25 cm and width of 50 cm (Figure 1). The site was in a lowland of mixed conifer-hardwoods in Ashland County, Wisconsin (latitude 46° 4' N, longitude 90° 38' W). Wolf 234M was detected on mortality mode at 1345, and the carcass was located at 1600 on 10 January; he had last been detected alive on 3 January 1996 1.6 km to the northeast.

The wolf was suffering from advanced stages of sarcoptic mange, and porcupine quills covered extensive areas of the body (Figure 2). Sarcoptic mange as well as heart failure and systemic infection appeared to be the main causes of death (N. J. Thomas, personal communication). At the time of death, 43-50 cm of snow covered the ground, and night temperatures were -24°C or lower.

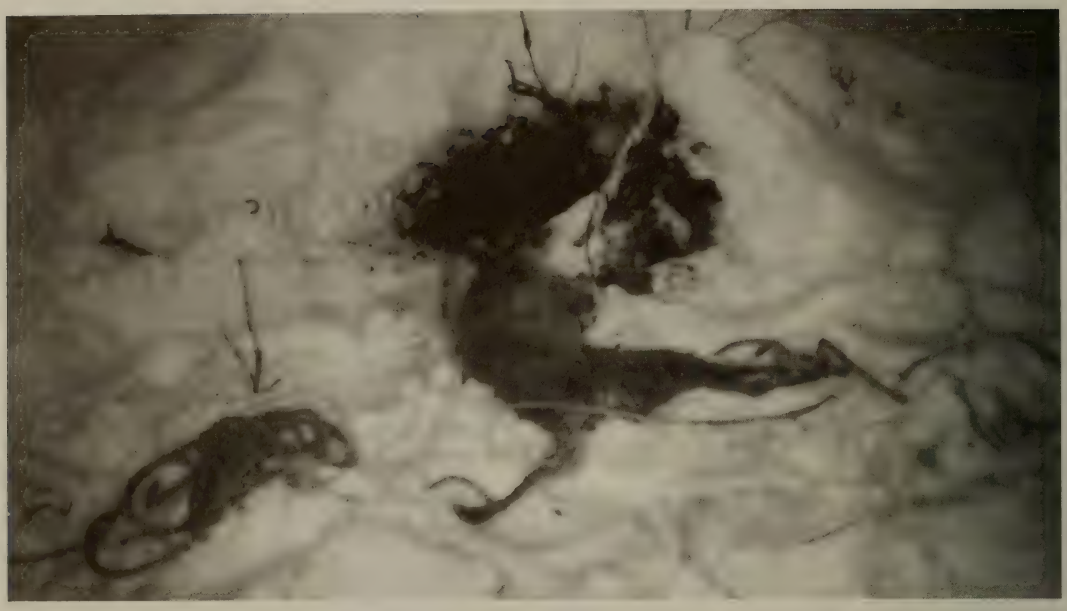


FIGURE 1. Dead wolf at entrance to Porcupine den in northern Wisconsin 10 January 1996.

Wolf 234M had been dead for 24 or more hours at the time the carcass was found. A Porcupine continued to visit the den site after the death of the wolf, as evident by urine and fresh Porcupine tracks at the entrance, and it may have just left the den site when we initially approached, and was observed about 20 m from the den. It is unknown whether the wolf had entered the den while the Porcupine was using it, or if the Porcupine had moved in after the wolf had occupied the den.

Two additional cases of wolf use and death in Porcupine dens have been observed in Wisconsin in recent years. On 17 December 1997 wolf 243F, the alpha female of the Miles Lake Pack in northeastern Price County (latitude 45° 59'N, longitude 90°6' W) was found dead in an uprooted White Cedar (*Thuja occidentalis*) cavity full of Porcupine droppings. The wolf had severe alopecia and apparently died due to the affects of sarcoptic mange. Her two pups had died from a combination of mange and parvovirus during the previous summer (N. J. Thomas, personal communication).

On 27 January 2000, a radio-collared female wolf was found dead in a Porcupine den at the base of a Silver Maple (*Acer saccharinum*) in the Bad River Indian Reservation of Ashland County (latitude 46° 28'N, longitude 90°6'W). The wolf had been the alpha female of the West Firelane Pack which consisted only of three wolves in early winter. All pack members were observed to have sarcoptic mange. The female wolf also apparently died from the effects of sarcoptic mange.

Sarcoptic mange was first identified in Great Lakes wolves in late 1991 (Wydeven et al. 1996), and seemed to affect most intensely the Wisconsin wolf population in 1992-1993 (Wisconsin Department of Natural Resources, 1999). Wolves affected by this disease appear to be willing to use any shelter available. Along with wolves dying inside of Porcupine dens, one adult female (203F) with severe alopecia died after being retrieved from a garage on 14 January 1993, and a yearling male (276M) was found dead in an old wolf den on 15 January 1998.

The use of Porcupine dens by wolves appears to be an extreme case of shelter-seeking behavior by individuals with advanced sarcoptic mange at the coldest time of the year. Because all the documented use of these Porcupine dens was by wolves that died, the behavior seemed to have minimum benefits. In 24 years of monitoring wolves in Wisconsin, we are unaware of healthy wolves using Porcupine dens. The use of their dens did not seem to disrupt the use of dens by Porcupines, which also share their dens with conspecifics during winter months (Griesemer et al. 1996).

Literature Cited

Griesemer, S. J., T. K. Fuller, and **R. M. Degraaf**. 1996. Denning patterns of porcupines, *Erethizon dorsatum*. Canadian Field-Naturalist 110: 634-637

Todd, A. W., J. R. Gunson, and **W. M. Samuel**. 1981. Sarcoptic mange: an important disease of coyotes and wolves of Alberta, Canada. Proceedings of Worldwide Furbearer Conference 1: 706-729.

Wisconsin Department of Natural Resources. 1999. Wisconsin Wolf Management Plan. Wisconsin Department of Natural Resources, PUBL-ER-0999, Madison, Wisconsin. 74 pages.

FIGURE 2. Wolf 234M, adult male, with severe alopecia due to sarcoptic mange and imbedded Porcupine quills, 10 January 1996.

Wydeven, A. P., R. N. Schulz, and **R. P. Thiel**. 1995. Monitoring of a recovering gray wolf population in Wisconsin, 1979-1991. Pages 147-156 *in* Ecology and Conservation of Wolves in a Changing World. *Edited by* L. N. Carbyn, S. H. Fritts, and D. R. Seip. Canadian Circumpolar Institute Occasional Publication Number 35. 642 pages.

Wydeven, A. P., K. Beheler-Amass, N. J. Thomas, R. N. Schultz, S. M. Schmitt, D. P. Shelley, and **T. M. Gehring**. 1996. Occurence of sarcoptic mange in Great Lakes States gray wolves (*Canus lupus*), 1991-1994. 14th Midwest Furbearer Workshop, Wakefield, Michigan, April 2-4.

Received 15 February 2001
Accepted 29 December 2003

Capture Locations of Coyotes, *Canis latrans*, Bobcats, *Lynx rufus*, and Raccoons, *Procyon lotor*, Relative to Home Range Boundaries

PHILIP S. GIPSON and JAN F. KAMLER[1]

Kansas Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, Division of Biology, 205 Leasure Hall, Kansas State University, Manhattan, Kansas 66506 USA
[1]Present address: Polish Academy of Sciences, Mammal Research Institute, 17-230 Bialowieża, Poland

Gipson, Philip S., and Jan F. Kamler. 2003. Capture locations of Coyotes, *Canis latrans*, Bobcats, *Lynx rufus*, and Raccoons, *Procyon lotor*, relative to home range boundaries. Canadian Field-Naturalist 117(3): 472-474.

Previous research showed that Coyotes (*Canis latrans*) and other canids might be more vulnerable to capture near the boundary or outside of their home ranges, making the capture of specific individuals within their territories difficult. Information concerning capture vulnerability relative to home range boundaries for other carnivores is lacking. During a four-year study of carnivore ecology in Kansas, we compared capture locations of Coyotes, Bobcats (*Lynx rufus*), and Raccoons (*Procyon lotor*) to their home range boundaries to determine if they were more likely to be captured inside, or near the periphery of, their home ranges. Resident Coyotes were captured disproportionately more often ($P < 0.01$) near the periphery of their home ranges, whereas Bobcats, Raccoons, and transient Coyotes were captured equally ($P > 0.05$) in both areas of their home ranges. Differences in capture vulnerability within and between species might be related to differences in social organization and behavior.

Key Words: Bobcat, *Lynx rufus*, Coyote, *Canis latrans*, Raccoon, *Procyon lotor*, capture locations, home range boundaries.

Some canid species, such as Coyotes (*Canis latrans*) and Red Foxes (*Vulpes vulpes*), have been shown to be most vulnerable to trapping near the periphery or outside of their home ranges (Hibler 1977; Woodruff and Keller 1982; Windberg and Knowlton 1990; Travaini et al. 1993; Sacks et al. 1999), although this has been disputed (Laundré and Keller 1983). Previous research suggests that peripheral areas are unfamiliar and used less by canids; thus canids are more prone to capture in these areas (Hibler 1977; Woodruff and Keller 1982; Harris 1983). Whether other carnivore groups, such as felids or procyonids, also are more vulnerable to trapping near the periphery of their home ranges is not known.

We conducted concurrent studies of Coyotes, Bobcats (*Lynx rufus*), and Raccoons (*Procyon lotor*) in northeastern Kansas from 1995 to 1999 (Kamler 1998). Our data allowed us to compare capture locations in relation to home range boundaries among these three species. Also, because age and social status were determined for study animals, we examined intraspecific differences in trapping vulnerability. Because differences in social organization, home range sizes, and habitat use are exhibited within and between these carnivore species (Sandell 1989; Kamler 1998), differences in trapping vulnerability also might occur.

Study Area and Methods

Data used in this paper were obtained during a study of predator interactions conducted on Fort Riley Military Reservation, Kansas (39°N, 97°W). Description of the study area is detailed in Kamler and Gipson (2000). At time of capture, we classified Coyotes as adult (> 2 years), yearling (1-2 years), or juvenile (< 1 year) based on body size, reproductive condition, and tooth wear (Gier 1968; Bowen 1982). We classified Bobcats as adult or juvenile based on body size, reproductive condition, and tooth replacement (Crowe 1975). We classified Raccoons as adult or juvenile based on body size, tooth wear, and for females, size and pigmentation of teats (Kaufmann 1982). From October 1995 to March 1999, we radio-collared and monitored 19 adult Coyotes, 10 adult Bobcats, and 12 adult Raccoons for this study. All animals, except four Raccoons captured in wire box traps, were captured in padded leghold traps. Most trapping occurred annually from October to March. Our capture and handling protocol, number 1098, was approved by the Institution Animal Use and Care Committee at Kansas State University.

Coyotes have been classified according to space use as "residents" and "transients" (Messier and Barrette 1982; Andelt 1985; Gese et al. 1988; Kamler and Gipson 2000). Home range sizes of Coyotes tend to be bimodally distributed, with home ranges of residents smaller than those of transients (Andelt 1985; Gese et al. 1988; Kamler and Gipson 2000). Therefore, we classified Coyotes as resident if they had relatively small home ranges (< 10 km^2) and associated with other Coyotes in the same areas, or transient if they had relatively large home ranges (> 20 km^2) and traveled alone (Andelt 1985). A large gap in home range sizes allowed for confident classifications of residents and transients (Kamler and Gipson 2000). Resident groups consist of a breeding pair and helpers (non-dispersing offspring) (Messier and Barrette 1982; Andelt 1985; Kamler and Gipson 2000). We classified resident Coyotes as breeders if they were located with adult Coyotes of the opposite sex on most occasions, especially during the breeding season, and if females were pregnant or nursing (Andelt 1985; Kamler and Gipson 2000). We classified resident Coyotes as helpers if they were yearling females that associated with a breeding pair, and showed no evidence of pregnancy during the reproductive season (Kamler and Gipson 2000).

Radio-telemetry methods are detailed in Kamler and Gipson (2000). We determined home range sizes for study animals by use of the minimum convex polygon (MCP) method (Mohr 1947), as calculated by CALHOME (Kie et al. 1994). We removed all capture and recapture locations and calculated home ranges for study animals with > 30 locations and > 6 months of radio-tracking. Data from only 13 Coyotes, 6 Bobcats, and 12 Raccoons met these criteria and were used in analyses. Trap locations in areas beyond 80% MCP home ranges were classified as "periphery," and those in areas within 80% MCP home ranges were classified as "inside." Although this classification is arbitrary, we believe that the 20% area near the outer edge of their home ranges adequately represents periphery areas. The 80% cutoff was between the 90% (Travaini et al. 1993) and 65% (Sacks et al. 1999) cutoff chosen by previous researchers. For each species, we used Yates-corrected chi-square goodness-of-fit tests to compare capture frequencies in the periphery and within home ranges to expected frequencies (20% and 80%, respectively).

Results

Home ranges were calculated for 13 adult Coyotes (seven residents and six transients). Seven resident Coyotes, five breeders and two helpers, were captured a total of eight times (one was captured twice) in the periphery or outside their home ranges (100%), as compared with 20% expected ($\chi^2 = 6.67$, $P < 0.01$). The two resident helpers were captured three times on excursions that were 1.8, 4.4, and 5.5 km away from their home range boundaries. Five of the six transient Coyotes were captured inside their home ranges (83%), as compared with 80% expected ($\chi^2 = 0.60$, $P = 0.44$). After more than 6 months, two transient Coyotes joined separate family groups and became resident Coyotes with home ranges that were 2.0 and 3.8 km from their initial capture location (Kamler and Gipson 2000).

Home ranges were calculated for six adult Bobcats captured a total of nine times (3 were captured twice). Eight captures were inside their home ranges (89%), as compared with 80% expected ($\chi^2 = 0.00$, $P = 1.00$). Home ranges were calculated for 12 Raccoons captured a total of 19 times (5 captured twice, 1 captured three times). Seventeen captures were inside their home ranges (89%), as compared with 80% expected ($\chi^2 = 0.20$, $P = 0.66$).

Discussion

We found that resident Coyotes were more likely to be captured in the periphery or outside of their home ranges, which is consistent with results of other studies (Hibler 1977; Woodruff and Keller 1982; Windberg and Knowlton 1990; Sacks et al. 1999). However, capture vulnerability relative to home range boundaries differed between social classes of Coyotes, as transients were captured proportionately throughout their home ranges. In contrast, Windberg and Knowlton (1990) found that 9 of 12 transient Coyotes were captured outside of their delineated home ranges. However, Windberg and Knowlton (1990) stated that their results were tenuous and that transients were only located 55% of the time, suggesting that delineated home ranges were incomplete. The transient Coyotes in our study were located > 90% of the time; therefore, delineated home ranges likely were more accurate.

Researchers have suggested that resident Coyotes were more vulnerable to capture in the periphery or outside of their home ranges because of less familiarity with those areas (Hibler 1977; Woodruff and Keller 1982; Harris 1983). However, because transient Coyotes, Bobcats, and Raccoons were not more likely to be captured near their home range boundaries, we believe that capture vulnerability of resident Coyotes might be more related to social behavior that results in greater inspection and marking of home range boundaries.

Social behavior of resident Coyotes includes group hunting, pair bonding, male care of young, and a high degree of territoriality with mutually exclusive home ranges among family groups (Kleiman and Eisenberg 1973; Andelt 1985; Windberg and Knowlton 1988). Transient Coyotes are solitary, non-reproducing, and have nomadic movement patterns that result in home ranges that are not well defined, non-territorial, and overlapping (Messier and Barrette 1982; Andelt 1985; Gese et al. 1988; Kamler and Gipson 2000). Social behavior of both Bobcats and Raccoons includes a solitary existence (except mother-young social units) and a low degree of territoriality with overlapping home ranges within and among sexes (Kleiman and Eisenberg 1973; Kaufmann 1982; Sandell 1989).

Group-living carnivores, such as resident Coyotes, maintain mutually exclusive family groups to ensure reproduction and rearing of young; thus regular inspection and marking of home range boundaries is necessary. Wells and Bekoff (1981) found that marking rates of resident male Coyotes were greatest in areas of high intrusion near home range boundaries, as opposed to denning areas and areas in which non-group members infrequently trespassed. Thus, Coyotes may expect to find new sign (such as trap sets) more in peripheral areas, as these areas are shared with neighboring family groups that might be attempting to encroach on their home ranges. However, new sign within core areas of Coyote family groups might be viewed as more unusual because these areas are not shared with other Coyotes, which could result in Coyotes being more wary of the new sign. Interestingly, Laundré and Keller (1981) showed that peripheral areas of Coyote home ranges could be high areas of use.

Inspection of new sign and marking in solitary carnivores, such as Bobcats and Raccoons, might occur equally in all parts of their home ranges because they

share most parts of their home range with other solitary individuals of the same species. Similar to resident Coyotes, some resident Bobcats and Raccoons in this study used the same areas for 3 years, thus were likely more familiar with areas within their home ranges than near the periphery. However, unlike resident Coyotes, Bobcats and Raccoons were not more likely to be captured in the periphery of their home ranges. Because transient Coyotes also had overlapping and non-territorial home ranges, they might inspect new sign and mark in a similar manner as solitary carnivore species. Because four Raccoons were captured in box traps baited with food, their captures might have been related to food acquisition and not necessarily inspection of new sign.

Resident Coyotes inspect new sign more intensely, and consequently might be more vulnerable to trapping, in peripheral areas because close inspection and marking are necessary to maintain territorial boundaries. We believe this is a more reasonable explanation for greater vulnerability of Coyotes near their territorial boundary, than lack of familiarity as suggested by others (Hibler 1977; Woodruff and Keller 1982; Harris 1983). Solitary carnivores, which do not have mutually exclusive home ranges and are not as territorial as resident Coyotes, might inspect new sign and mark equally throughout all areas of their home ranges. Thus, solitary carnivores might be equally vulnerable to trapping throughout their home ranges.

Acknowledgments

This project was funded by U.S. Department of Defense, in cooperation with Kansas Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, and Division of Biology at Kansas State University. Comments by G. Batcheller, R. Belden, and M. Chamberlain helped improve this manuscript. We thank D. Jones, H. Abel, M. Pont, C. Richardson and other personnel at the Conservation Division on Fort Riley for their assistance. We also thank J. Beckman, B. Bowman, J. Goheen, D. Hogan, B. Kamler, C. Perchellet, T. Snyder, C. Richardson, and G. Truan for assistance with field work and other aspects of the project.

Literature Cited

Andelt, W. F. 1985. Behavioral ecology of coyotes in south Texas. Wildlife Monographs 94. 45 pages.

Bowen, W. O. 1982. Determining age of coyotes, *Canis latrans*, by tooth sections and tooth wear patterns. Canadian Field-Naturalist 96: 339-341.

Crowe, D. M. 1975. Aspects of aging, growth and reproduction of bobcats in Wyoming. Journal of Mammalogy 56: 177-198.

Gese, E. M., O. J. Rongstad, and **W. R. Mytton.** 1988. Home range and habitat use of coyotes in southeastern Colorado. Journal of Wildlife Management 52: 640-646.

Gier, H. T. 1968. Coyotes in Kansas. Revised. Kansas State College Agricultural Experiment Station Bulletin 393. 97 pages.

Harris, C. E. 1983. Differential behavior of coyotes with regard to home range limits. Ph.D. dissertation. Utah State University, Logan. 120 pages.

Hibler, S. J. 1977. Coyote movement patterns with emphasis on home range characteristics. M.S. thesis, Utah State University, Logan. 112 pages.

Kamler, J. F. 1998. Ecology and interspecific relationships of mammalian predators on Fort Riley Military Reservation, Kansas. M.S. thesis, Kansas State University, Manhattan. 150 pages.

Kamler, J. F., and **P. S. Gipson.** 2000. Space and habitat use by resident and transient coyotes. Canadian Journal of Zoology 78: 2106-2111.

Kaufmann, J. H. 1982. Raccoon and allies. Pages 567-585 *in* Wild mammals of North America. *Edited by* J. A. Chapman and G. A. Feldhamer. The Johns Hopkins University Press, Baltimore, Maryland.

Kie, J. G., J. A. Baldwin, and **C. J. Evans.** 1994. CALHOME: home range analysis program. U.S. Forest Service, Pacific Southwest Research Station, Fresno, California. 19 pages.

Kleiman, D. G., and **J. F. Eisenberg.** 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Animal Behaviour 21: 637-659.

Laundré, J. W., and **B. L. Keller.** 1981. Home range use by coyotes in Idaho. Animal Behaviour 19: 449-461.

Laundré, J. W., and **B. L. Keller.** 1983. Trappability of coyotes relative to home range boundaries. Canadian Journal of Zoology 61: 1932-1934.

Messier, F., and **C. Barrette.** 1982. The social system of the coyote (*Canis latrans*) in a forested habitat. Canadian Journal of Zoology 60: 1743-1753.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37: 223-249.

Sacks, B. N., K. M. Blejwas, and **M. M. Jaeger.** 1999. Relative vulnerability of coyotes to removal methods on a northern California ranch. Journal of Wildlife Management 63: 939-949.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164-182 *in* Carnivore behavior, ecology, and evolution, volume 1. *Edited by* J. L. Gittleman. Cornell University Press, Ithaca, New York.

Travaini, A., J. Aldama, and **M. Delibes.** 1993. Red fox capture locations in relation to home range boundaries. Mammalia 57: 448-451.

Wells, M. C., and **M. Bekoff.** 1981. An observational study of scent-marking in coyotes, *Canis latrans*. Animal Behaviour 29: 332-350.

Windberg, L. A., and **F. F. Knowlton.** 1988. Management implications of coyote spacing patterns in southern Texas. Journal of Wildlife Management 52: 632-640.

Windberg, L. A., and **F. F. Knowlton.** 1990. Relative vulnerability of coyotes to some capture procedures. Wildlife Society Bulletin 18: 282-290.

Woodruff, R. A., and **B. L. Keller.** 1982. Dispersal, daily activity, and home range of coyotes in southeastern Idaho. Northwest Science 56: 199-207.

Received 5 July 2001
Accepted 24 March 2004

The Chain Dogfish, *Scyliorhinus retifer* (Garman, 1881), New to the Canadian Atlantic Ichthyofauna

GILHEN, JOHN[1], BRIAN W. COAD[2] and ANDREW HEBDA[1]

[1] Nova Scotia Museum of Natural History, 1747 Summer Street, Halifax, Nova Scotia B3H 3A6 Canada
[2] Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa K1P 6P4 Canada

Gilhen, John, Brian W. Coad, and Andrew Hebda. 2003. The Chain Dogfish, *Scyliorhinus retifer* (Garman, 1881), New to the Canadian Atlantic Ichthyofauna. Canadian Field- Naturalist 117(3): 475-477.

The Chain Dogfish, *Scyliorhinus retifer*, is known from southwestern Georges Bank in the United States but until now there have been no verifiable records of this shark in Canadian waters. We report on two specimens Georges Bank, Big LaHave Bank, Nova Scotia, that represent the first and second records for the Canadian Atlantic.

Key Words: Chain Dogfish, *Scyliorhinus retifer*, first records, Canadian Atlantic.

The Chain Dogfish, *Scyliorhinus retifer*, is a member of the Cat Shark Family (Scyliorhinidae) found from the United States south to Nicaragua. It is distinguished from its Atlantic coast relatives by having crests over the eyes and by a chain or net body pattern. There has been no confirmed record for Canadian waters although Coad et al. (1995) report it from southwestern Georges Bank in American waters based on Bigelow et al. (1953). This paper reports the presence of this shark in Canadian waters based on two specimens from Nova Scotia.

Methods and Materials

Counts and measurements follow Hubbs and Lagler (1964) and Springer (1979). Abbreviations are TL = total length; NSM = Nova Scotia Museum of Natural History, Halifax. NSM85357, female, 37.5 cm TL, 253.7 g, Nova Scotia, Georges Bank, 1980s (kept on ice for seven days in a display at the Lunenburg Fisheries Exhibition in Lunenburg, Nova Scotia; captured by the Canadian scallop fishery). NSM85352, female, 38.6 cm TL, 219.7 g, Nova Scotia, southern outer edge of Big LaHave Bank, 42° 32'00"N, 64° 32'00"W, captured with Silver Hake, *Merluccius bilinearis*, in an otter trawl between 140 and 200 fathoms, 10 May 2001, David A. D'Eon (Captain of the trawler *Seamans Toy* out of Lower West Pubnico).

Results

The body is slender with a wedge-shaped snout, although the belly may be distended with food. The nasal flaps do not reach the edge of the upper lip. Crests are present over the eyes. Teeth are triangular, smooth and have a long central cusp with a smaller cusp on each side. Denticles on the flank are small, lanceolate and flat.

FIGURE 1. An adult female Chain Dogfish, *Scyliorhinus retifer*, first record for the Canadian Atlantic, captured on Georges Bank, Nova Scotia, in the 1980s (Nova Scotia Museum of Natural History Negative Number N-25,643).

FIGURE 2. An adult female Chain Dogfish, *Scyliorhinus retifer*, second record for the Canadian Atlantic, captured at the southern outer edge of Big LaHave Bank, Nova Scotia, 10 May 2001, by David A. D'Eon (Nova Scotia Museum of Natural History Negative Number N-25,642).

Measurements after Springer (1979) for the two specimens are as follows in percentages of total length: tip of snout to front of mouth 4.8-4.9; to eye 6.4-6.7; to first gill slit 15.4-15.5; to fifth gill slit 19.0-19.9; to origin of pectoral fin 18.3-19.6; to origin of first dorsal fin 51.5-52.5; to origin of pelvic fin 43.2-44.6; to second dorsal fin 67.0-69.0; to anal fin 61.5-63.1; to origin of upper caudal fin lobe 77.5-78.7; to anterior end of cloacal opening 45.3-47.2. Orbit diameter 3.8-3.9 and orbit height 0.9-1.0. Least distance between nasal apertures 1.7. Mouth width 8.0-8.2 and mouth length 4.0-5.0. Length lower labial furrow 1.4. Height of first gill slit 1.8-2.0 and height of fifth gill slit 0.7-1.1. First dorsal fin base length 6.0-6.7 and anterior margin length 9.9. Second dorsal fin base length 4.9-5.6 and anterior margin length 7.3-7.7. Anal fin base length 6.5-7.6 and anterior margin length 7.4-7.6. Length outer margin of pectoral fin 13.2-14.1. Distance between first and second dorsal fin bases 10.4-11.1.

The chain pattern of narrow black lines forming 7 (7-8 in the literature) dorsal saddles is distinctive and is illustrated in Figures 1 and 2. In preservative NSM-85352 is grey with black chain markings while NSM-85357 is brown with dark brown chain markings.

Discussion

The two specimens agree generally with the description of this species in Springer (1979) and Springer and Sadowsky (1970), being females of the subspecies *S. retifer retifer*. This subspecies reaches a maximum size of over 52.0 cm in females. Females may mature at 38.0 cm, perhaps larger. Males are mature at about 30.0-50.0 cm. Northern populations may mature at a smaller size than southern ones, and one of these Canadian specimens was approaching maturity (NSM-85357 has eggs about 1.2 cm in diameter). This species inhabits rough bottoms, not easily trawled, as well as smooth bottoms, from 58 m to 550 m on the continental shelf and upper slope. Some were associated with anemones. Water temperatures are 8.5-14.0°C and lower temperatures may limit its occurrence in Canada. Stomach contents include squids (NSM85357 contains a squid), fishes, worms and crustaceans. Some were reported to have pebbles in the stomach. There are 6-20 ova up to 1.8 cm in diameter in a single, left ovary. Egg cases, up to 6.3 by 2.7 cm with long tendrils, are deposited on hard substrates or attached to hydrozoans attached to such substrates (Springer and Sadowsky 1970; Springer 1979; Castro et al. 1988; Able and Flescher 1991; Coad et al. 1995).

Acknowledgments

We are grateful to Captain David A. D'Eon, Lower West Pubnico, Yarmouth County, Nova Scotia, who collected the second Chain Dogfish and donated it to the Nova Scotia Museum of Natural History. We thank Albert D'Entremont, science teacher, at Saint Anne du Ruisseau School, West Pubnico, who is an important liaison between the fishers of West Pubnico and the Nova Scotia Museum of Natural History. Over the years he has held in frozen storage many important marine specimens which he receives from local fishers, including our second Chain Dogfish (NSM85352), until they can be brought to the Nova Scotia Museum of Natural History to be identified, catalogued and preserved for future study.

The photographs, Figures 1 and 2, are by Roger Lloyd, Learning Resources and Technology, Nova Scotia Department of Education.

Literature Cited

Able, K. W., and **D. Flescher.** 1991. Distribution and habitat of chain dogfish, *Scyliorhinus retifer*, in the mid-Atlantic Bight. Copeia 1991: 231-234.

Bigelow, H. B., W. C. Schroeder, and **S. Springer.** 1953. New and little known sharks from the Atlantic and from the Gulf of Mexico. Bulletin of the Museum of Comparative Zoology 109(3): 213-276.

Castro, J. I., P. M. Bubucis, and **N. A. Overstrom.** 1988. The reproductive biology of the chain dogfish, *Scyliorhinus retifer*. Copeia 1988: 740-746.

Coad, Brian W., H. Waszczuk, and **I. Labignan.** 1995. Encyclopedia of Canadian Fishes. Canadian Museum of Nature, Ottawa, and Canadian Sportfishing Productions, Waterdown, Ontario. viii + 928 pages

Hubbs, C. L., and **K. F. Lagler.** 1964. Fishes of the Great Lakes Region. The University of Michigan Press, Ann Arbor. xv + 213 pages

Springer, S. 1979. A revision of the catsharks, Family Scyliorhinidae. NOAA (National Oceanographic and Atmospheric Administration, NMFS (National Marine Fisheries Service) Circular 422: v + 152 pages

Springer, S., and **V. Sadowsky.** 1970. Subspecies of the western Atlantic cat shark, *Scyliorhinus retifer*. Proceedings of the Biological Society of Washington 83: 83-98.

Received 31 August 2001
Accepted 2 January 2004

First Record of Mink Frog, *Rana septentrionalis*, from Insular Newfoundland

IAN G. WARKENTIN[1], CHRISTINE E. CAMPBELL[1], KRISTIN G. POWELL[1, 2] and TINA D. LEONARD[1, 2]

[1]Environmental Science, Sir Wilfred Grenfell College, Memorial University of Newfoundland, Corner Brook, Newfoundland A2H 6P9 Canada
[2]Department of Biology, Acadia University, Wolfville, Nova Scotia B4P 2R6 Canada

Warkentin, Ian G., Christine E. Campbell, Kristin G. Powell, and Tina D. Leonard. 2003. First record of the Mink Frog (*Rana septentrionalis*) from insular Newfoundland. Canadian Field-Naturalist 117(3): 477-478.

Two populations of the Mink Frog (*Rana septentrionalis*) were identified near Corner Brook, Newfoundland, during wider surveys for anurans on the west coast of the island. This brings to six the number of anuran species which are known to have been introduced to insular Newfoundland, with four known to be currently extant.

Key Words: Mink Frog, *Rana septentrionalis*, Newfoundland, introduced species.

The anuran fauna of insular Newfoundland is the result of intentional human introductions. The Green Frog (*Rana clamitans*) arrived about 150 years ago through its presumed accidental transport in shipments of hay from Nova Scotia to the St. John's area (Maret 1867; Johansen 1926). Between 1960 and 1966, Buckle (1971) systematically introduced the Northern Leopard Frog (*Rana pipiens*), Wood Frog (*R. sylvatica*), Chorus Frog (*Pseudacris triseriata*) and American Toad (*Bufo americanus*) to various locations in western Newfoundland. These anuran populations have since undergone extensive change. Both the Northern Leopard Frog and the Chorus Frog apparently have disappeared (Maunder 1997), but populations of the other three species are now well established and are expanding throughout the western portion of the island (Maunder 1997; Powell 2002). The Green Frog remains the sole anuran occupant of eastern portions of the island (Maunder 1997). Here we report the discovery on the west coast of the island of another introduced anuran, the Mink Frog (*Rana septentrionalis*).

Field work was conducted in summer 2001 to assess the distribution of anuran populations in three regions along the west coast of Newfoundland – the Codroy Valley in the southwestern corner of the island, the Deer Lake-Stephenville region in west-central Newfoundland, and Gros Morne National Park on the west coast of the island at the base of the Great Northern Peninsula. American Toads were heard at numerous locations in all three regions, Wood Frogs were heard throughout the Deer Lake-Stephenville region, while Green Frogs were heard throughout the Deer Lake-Stephenville and Codroy Valley regions and at one location in Gros Morne National Park (Powell 2002). We encountered Mink Frogs at one site in the Deer Lake-Stephenville region. Located along the Ring Road of Corner Brook, 4.8 km west of the Trans Canada Highway (48° 55.61'N, 57° 57.11'W; all positions determined using a Garmin® GPS model 12 XL, Olathe Kansas, USA), the site consists of a shallow pond approximately 60 m long by 10 m at its widest point. The presence of the frogs was initially detected during daylight hours on 30 May 2001, and on a return visit later that day in excess of 30 Mink Frogs were counted in a 10 m^2 area on one end of the pond. Additionally, Powell (2002) found 25 Mink Frog tadpoles along a 10-m stretch of pond shoreline at this site on 30 June 2001.

Although Mink Frog adults are considered by some to strongly resemble the appearance of Green Frogs at the northern end of their range (Conant and Collins 1991), there are several distinctive features of *R. septentrionalis* including the mink-like smell, spotting pattern on the legs, the extent of dorsolateral ridges, and the extreme webbing on the toes of the hind feet (Schueler 1975; Conant and Collins 1991). In combination, these characteristics enabled us to distinguish Mink Frog adults from morphologically similar Green Frogs. Voucher specimens were collected and deposited at the Provincial Museum of Newfoundland and Labrador in St. John's, Newfoundland (Provincial Museum catalogue numbers NFM HE-119 and NFM HE-120).

Species identification was confirmed through nighttime calling surveys. At 2300 h on 14 and 15 June 2001, sufficient individuals were heard to constitute a chorus of indistinguishable, overlapping calls (calling index of 3 based on the Frogwatch USA Program; www.mp2pwrc.usgs.gov/NAAMP/protocol/definitions.html#index). These frogs were calling from a location about 50 m across the pond from the original position where they were seen during the day on 30 May 2001. Again, on the night of 21 June 2001, Mink Frogs were heard calling from this site (4 individuals) as well as at a location 1600 m further west (48° 55.70'N, 57° 58.34' W) where two individuals were heard calling from a stream which runs through a fen beside the Ring Road. Earlier that day (1330 h) full choruses of Mink Frogs were heard at both of these sites.

Subsequently, and apart from our regular survey sites identified for the larger study, Mink Frogs also were heard calling at four locations along the Cook's Brook drainage on the nights of 18 and 21 June 2001: (1) at the inflow of Cook's Brook into the southern end of Big Cook's Pond (3 individuals heard on 21 June; 48° 51.75'N, 58° 4.81'W), (2) at the outflow of Cook's Brook from Little Cook's Pond (4 individuals heard 18 June, 1 individual 21 June; 48° 53.51'N, 58° 3.69'W), (3) along Cook's Brook about 900 m downstream from Little Cook's Pond (6 Mink Frogs and 4 Green Frogs on 18 June, 2 Mink Frogs on 21 June; 48° 53.78'N, 58° 3.26'W), and (4) a small pond (5 m across) near where Burnt Creek empties into Cook's Brook and 6.3 km from the Big Cook's Pond site (2 mink frogs heard on 18 June; 48° 54.93'N, 58° 3.34'W). American Toads were heard at all locations along Cook's Brook. This area along Cook's Brook is about 8 km distant from the Corner Brook Ring Road sites in an adjacent drainage, suggesting the possibility of at least two initial release sites, or release and subsequent translocation.

Mink Frogs were not detected at the other 29 of our 30 survey sites in the Deer Lake-Stephenville region, nor at any of the 60 sites in the Codroy Valley and Gros Morne National Park. All sites for the more extensive survey were visited on three occasions (7-16 May, 28 May – 6 June, 28 June – 6 July 2001) both during the day for egg mass and tadpole surveys and during the night for calling surveys. Previous searches (Maunder 1983, 1997) did not detect Mink Frogs on the island. Together, these data suggest that the release of Mink Frogs may have been recent. While source populations for past acknowledged introductions of anurans to the west coast of the island were from southern Ontario (Buckle 1971), it is possible that Mink Frogs may have been introduced from native populations in Labrador. When questioned, no members of the local community admitted to introducing this additional species.

Acknowledgments

Funding was provided to Kristin Powell through a University Internship in Environmental Science sponsored by Gros Morne National Park and the Gros Morne Co-operating Association; additional support came from Sir Wilfred Grenfell College through the Environmental Science Study and Travel Grants program and a Summer Undergraduate Research Award. Voucher specimens were collected under permit issued by Leah Soper of the Newfoundland and Labrador Department of Forest Resources and Agrifoods; John Maunder provided the catalogue numbers from the Provincial Museum.

Literature Cited

Buckle, J. 1971. A recent introduction of frogs to Newfoundland. Canadian Field-Naturalist 85: 72-74.

Conant, R. and **J. T. Collins.** 1991. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin Company, Boston.

Johansen, F. 1926. Occurrences of frogs on Anticosti Island and Newfoundland. Canadian Field-Naturalist 40: 16.

Maret, E. 1867. Frogs on Newfoundland. Proceedings of the Nova Scotian Institute of Science 1: 6.

Maunder, J. E. 1983. Amphibians of the Province of Newfoundland. Canadian Field-Naturalist 97: 33-46.

Maunder, J. E. 1997. Amphibians of Newfoundland and Labrador: status changes since 1983. Herpetological Conservation 1: 93-99.

Powell, K. G. 2002. Watersheds and water quality as determinants of anuran distribution in western Newfoundland. B.Sc. Honours thesis, Memorial University of Newfoundland, Corner Brook, Newfoundland. 65 pages.

Schueler, F. W. 1975. Geographic variation in the size of *Rana septentrionalis* in Quebec, Ontario, and Manitoba. Journal of Herpetology 9: 177-185.

Received 30 July 2001
Accepted 1 April 2004

Northern Harrier, *Circus cyaneus,* Attacks on Greater Sage-Grouse, *Centerocercus urophasianus,* in Southern Alberta

QUINN E. FLETCHER[1], CRAIG W. DOCKRILL, D. JOANNE SAHER, and CAMERON L. ALDRIDGE[2]

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9 Canada
[1]Current Address: Department of Life Sciences, University of Toronto at Scarborough, 1265 Military Trail, Scarborough, Ontario M1C 1A4 Canada
[2]Corresponding Author: e-mail: aldridge@ualberta.ca

Fletcher, Quinn E., Craig W. Dockrill, D. Joanne Saher, and Cameron L. Aldridge. 2003. Northern Harrier, *Circus cyaneus,* attacks on Greater Sage-Grouse, *Centerocercus urophasianus,* in southern Alberta. Canadian Field-Naturalist 117(3): 479-480.

The Greater Sage-Grouse (*Centrocercus urophasianus*) is an endangered species in Canada, making it critical to understand all known causes of mortality. We report the first recorded observations of female Northern Harrier (*Circus cyaneus*) attacks on male Greater Sage-Grouse. Although no attacks were successful, our observations suggest that Northern Harriers are predators of Greater Sage-Grouse.

Key Words: Greater Sage-Grouse, *Centrocercus urophasianus*, Northern Harrier, *Circus cyaneus*, endangered species, lek, predation, Alberta

Northern Harriers (*Circus cyaneus*) are opportunistic predators that use visual and auditory cues to locate their prey (MacWhirter and Bildstein 1996). Rodents, passerines, small water birds, reptiles and frogs are the principal prey of harriers (Collopy and Bildstein 1987); however, prey choices are ultimately limited only by the size, formidability, and availability of prey (MacWhirter and Bildstein 1996). Northern Harriers are a sexually dimorphic species with females (432-621 g) being larger than males (308-387 g) (MacWhirter and Bildstein 1996), making them more capable of capturing larger prey items. The largest known avian prey taken by Northern Harriers weigh < 1300g [Sharp-tailed Grouse (*Tympanuchus phasianellus*) – 880 g (Connelly et al. 1998); male Ring-necked Pheasants (*Phasianus colchicus*) – 1250 g (Dale 1956)]; approximately twice the weight of a female Northern Harrier. As most studies of harrier prey selection are based on observations of prey delivery to nests (MacWhirter and Bildstein 1996), the relative importance of prey too heavy to carry back to the nest may be underestimated.

The Greater Sage-Grouse (*Centrocercus urophasianus*) is an endangered species in Canada. Golden Eagles (*Aquila chrysaetos*), Ferruginous Hawks (*Buteo regalis*), Red-tailed Hawks (*Buteo jamaicensis*), Swainson's Hawks (*Buteo swainsoni*), Gyrfalcons (*Falco rusticolus*), Northern Goshawks (*Accipiter gentilis*), and Great Horned Owls (*Bubo virginianus*) are known avian predators of adult sage-grouse (Schroeder et al. 1999; CLA personal observation). Northern Harriers are known to prey on the chicks of Greater Sage-Grouse, but there are no known records of predation on adults (Schroeder et al. 1999). Here we report predation attempts by female Northern Harriers on adult male sage-grouse. Male sage-grouse have an average mass of 3122 g (n = 48, Aldridge 2000) in southeastern Alberta, suggesting that potential prey of harriers may be almost three times heavier than previously reported.

Observations

Breeding displays of male Greater Sage-Grouse take place at both dawn and dusk at breeding arenas (leks), with the most intense displays occurring in the hour immediately surrounding sunrise (Jenni and Hartzler 1978). As part of ongoing research on Greater Sage-Grouse in southeastern Alberta, we conducted morning lek censuses between 24 March and 24 May 2001. Each census consisted of observing the breeding activities for 20 to 40 minutes. We repeatedly observed all seven known active leks for an average of 23 ± 6.6 visits to each lek. During the course of these counts, we made the following observations.

On 8 April 2001, the carcass of a male Greater Sage-Grouse was found on a lek. The sage-grouse was decapitated and most of the carcass was consumed. The feathers were plucked, and exhibited crimp marks. Raptors often pluck the feathers of their prey, crimping the shaft, and commonly decapitate the prey item, selecting the neck and breast meat of the bird (Einarsen 1900).

Two days later on the same lek (10 April 2001), a female Northern Harrier attempted an attack on several male Greater Sage-Grouse. As the harrier approached the lek, all nine males present stopped displaying and crouched down. The harrier dove at one sage-grouse, which responded by flying from the lek when the harrier was *ca.* 5 m away. The harrier pursued the grouse for about 10 m, but the attack was unsuccessful. The harrier then turned and flew back to the center of the lek causing the remaining eight sage-grouse to fly from lek. The male sage-grouse did not return to the lek and breeding activities were interrupted for the remainder of the morning.

A similar incident occurred at a second lek site on 4 May 2001, when a female harrier swooped over male sage-grouse on the lek site without diving or focusing an attack on a single individual. In response, nine of the 23 males that were displaying flew from the lek,

and the remaining 14 sage-grouse stopped displaying and crouched close to the ground.

Discussion

Our observations suggest that Northern Harriers may be predators of adult male Greater Sage-Grouse. Furthermore, the defensive behaviours exhibited by male sage-grouse in response to Northern Harrier attacks parallel sage-grouse responses to attacks by Golden Eagles (Hartzler 1974; Ellis 1984), indicating that Greater Sage-Grouse recognize Northern Harriers as predators.

Northern Harriers appear to be potential predators of adult Greater Sage-Grouse and may frequent lek locations to exploit high concentrations of grouse during the breeding season. Harriers in Scotland display similar behaviours, selectively hunting in habitats with high abundances of Red Grouse (*Lagopus lagopus*; Redpath 1992). Given that most sage-grouse populations are declining and that predation is considered the primary source of mortality for prairie grouse (Schroeder and Baydack 2001), the identification of predators is essential to conservation and population management efforts, especially for the endangered Canadian Greater Sage-Grouse population.

Acknowledgments

This research was possible because of financial and/or logistical contributions from the following organizations: Alberta Conservation Association, Alberta Sustainable Resource Development, Alberta Sport Recreation Parks and Wildlife Foundation, Canadian Wildlife Foundation, Ducks Unlimited Canada (North American Waterfowl Management Plan), Challenge Grants in Biodiversity (University of Alberta), Endangered Species Recovery Fund (World Wildlife Fund Canada and the Canadian Wildlife Service), a Natural Science and Engineering Research Council Scholarship to C.L. Aldridge, and the University of Alberta. We are appreciative of the many individuals and families who gave us permission to work on their land throughout the course of our research. We thank M. M. Humphries, R. G. Poulin, M. S. Boyce, A. J. Erskine, and C. S. Houston for comments on previous drafts of this manuscript.

Literature Cited

Aldridge, C. L. 2000. Reproduction and habitat use by Sage Grouse (*Centrocercus urophasianus*) in a northern fringe population. M.Sc. thesis. University of Regina, Regina, Saskatchewan. 109 pages.

Collopy, M. W., and **K. L. Bildstein.** 1987. Foraging behavior of Northern Harriers wintering in southeastern salt and freshwater marshes. Auk 104: 11-16.

Connelly, J. W., M. W. Gratson, and **K. P. Reese.** 1998. Sharp-tailed Grouse (*Tympanuchus phasianellus*) *in* The birds of North America, Number 354. *Edited by* A. Pool and F. Gill. The Birds of North America, Inc., Philadelphia, Pennsylvania. 20 pages.

Dale, F. H. 1956. Pheasants and Pheasant Populations. Pages 1-42 *in* Pheasants in North America. *Edited by* D. L. Allen. Stackpole Company, Harrisburg, Pennsylvania.

Einarsen, A. S. 1900. Determination of some predator species by field signs. Oregon State College Publications in Biology, Oregon Monographs. 36 pages.

Ellis, K. L. 1984. Behavior of a lekking Sage Grouse in response to a perched Golden Eagle. Western Birds 15: 37-38.

Hartzler, J. E. 1974. Predation and the daily timing of Sage Grouse leks. Auk 91: 532-536.

Jenni, D. A., and **J. E. Hartzler.** 1978. Attendance at a Sage Grouse lek: implications for spring censuses. Journal of Wildlife Management 42: 46-52.

MacWhirter, R. B., and **K. L. Bildstein.** 1996. Northern Harrier (*Circus cyaneus*) *in* The Birds of North America, Number 210. *Edited by* A. Pool and F. Gill. The Birds of North America, Inc., Philadelphia, Pennsylvania. 31 pages.

Redpath, S. M. 1992. Behavioural interactions between Hen Harriers and their moorland prey. Ornis Scandinavica 23: 73-80.

Schroeder, M. A., J. R. Young, and **C. E. Braun.** 1999. Sage Grouse (*Centrocercus urophasianus*) *in* The Birds of North America, Number 425. *Edited by* A. Pool and F. Gill. The Birds of North America, Inc., Philadelphia, Pennsylvania. 28 pages.

Schroeder, M. A., and **R. K. Baydack.** 2001. Predation and the management of prairie grouse. Wildlife Society Bulletin 29: 24-32.

Received 22 January 2002
Accepted 30 March 2004

A Tribute to Clarence Frankton 1906-2000

DANIEL F. BRUNTON

216 Lincoln Heights Road, Ottawa, Ontario K2B 8A8 Canada

Brunton, Daniel F. 2003. A tribute to Clarence Frankton 1904-2000. Canadian Field-Naturalist 117(3): 481-486.

Two events which say much about the way botanist Clarence ("Clarrie') Frankton viewed the world and the study of its natural environment occurred in mid-May 2000, only weeks before his death 11 June. Although succumbing to the ravages of cancer and strokes which left him confined to his west-end Ottawa, Ontario home, he could only be described as "chipper" and even buoyant when botanical discoveries were put before him. Days earlier he had directed his wife Enid back to the shores of the Ottawa River to collect a particular specimen. Clarrie had been working on the identity of this nondescript shrub since the previous fall and he was sure it would be in flower now. It was, and despite his substantial physical challenges, he worked the specimen through and determined it to be *Prunus americana*, precisely the rare (for the Ottawa Valley) introduced taxon that he had argued for all along. And in light of my earlier skepticism regarding that possibility, he made sure I was reminded right away how it all had turned out. His playful and inspiring competitiveness, however, was just as quickly put aside a few days later as he lauded the discovery of a locally rare native species (*Cardamine bulbosa*) and enthusiastically assessed the implications of the find. Clarrie was like that, always looking forward, always building upon what he already knew, always keenly anticipating the new challenge ahead.

His long-ago British beginnings were subtly, elegantly evident in his speech, with fine pronunciation and the frequent use of phrases like "*quite so*" and "*there you have it*". He was born on 6 February 1906 in Nottingham, England. His parents, William and Louise, immigrated with their only son to Montreal in 1914. William Frankton worked thereafter as an accountant for the Canadian Pacific Railway. They enjoyed a modest and happy residence in East-end Montreal and seemingly very much enjoyed that community. One of Clarrie's earliest Canadian memories was of going for a long walk with his father one day to hear a well-known politician rouse an East-end crowd into partisan fervour. The place was likely Parc Lafontaine. The politician was certainly Sir Wilfrid Laurier. Clarrie was suitably impressed and recounted the event many years later with both clarity and enthusiasm.

He left commercial high school early because of a lack of money to support continued studies and worked as an office boy at the Sun Life Insurance Company in downtown Montreal. Nonetheless, he studied privately and wrote the high school final exams, achieving the highest score in mathematics in the province of Quebec that year. He also employed his lifelong love of mathematics to good purpose while working for a time as a night accountant at the famed Algonquin Hotel in

Clarrie Frankton in Montreal Amateur Athletic Association uniform ca. 1932 (photo courtesy of Enid Frankton)

St. Stephen, New Brunswick. His daughter Gwen (Coffin) aptly described his mathematical passion in her tribute delivered at a well-attended remembrance celebration in June 2000 " ... he loved the idea of it, loved its practice. He really enjoyed doing his taxes ! In the hospital after his first stroke he was reading *Mathematics for the Millions*, a loved and tattered volume".

When finances permitted, Clarrie entered into the general B. Sc. program at McGill University where he soon discovered an interest in botany. Despite an enjoyment of countryside rambles, neither his parents nor personal associates directly inspired his subsequent calling. He came to that discovery in undergraduate school, soon delighting in botany as a science and in field-based research as an approach. He was spurred to take an ecological, interdisciplinary view of botanical questions by several prominent professors of the day, including F. E. Lloyd, G. W. Scarth and V. C. Wynne-Edwards. He graduated with a Ph.D. from McGill in 1946, his doctoral thesis addressing the ecology of pasture grasses of Quebec.

Up to and throughout his university years, Clarrie was also a serious and highly successful long-distance runner and a member of the renowned Montreal Amateur Athletic Association. He accumulated a remarkable number of ribbons, medals and trophies during this period for victories in various cross country categories. And this racing went on year round too, as he also competed in winter on snowshoes. On at least one occasion in the 1930s he won the World Snowshoe Championships conducted during the Quebec Winter Fair. Clarrie remained astonishingly fit and a keen "walker" into his 90s. He was quite capable and mischievously keen to walk much younger associates into the ground when he was in his mid-80s. (I can present scars as proof!). He held absolutely no fear of bush-whacking, be that through marsh, buckthorn thicket or seemingly impenetrable cedar bush, if there was the promise of a good plant record in it.

When he completed his university studies Clarrie first found employment conducting pasture research with the Quebec Department of Agriculture, much of his field work being conducted in the Eastern Townships. His recall of events, sites and discoveries in those years was uncanny. These bits of understanding were regularly brought forward decades later, not as "good old days" reminiscences but as pertinent insights to be effectively applied to a question before us in the present day.

Clarrie's provincial Department of Agriculture employment ended in 1946 when he resigned to protest a maneuver which apparently saw the replacement of his supervisor (Dr. Carl Raymond) with a political appointee. While visiting the Botany Department at McGill shortly thereafter, however, and "*in between positions*" as he later put it, he struck up a conversation with Harold Senn, visiting head of the Botany Unit of the federal Department of Agriculture (later, Agriculture Canada) at the Central Experimental Farm in Ottawa, Ontario. Senn, who recruited a remarkable team of field botanists and taxonomists during the 1940s and early 1950s (Cody 1997), was obviously impressed. Two days later a letter arrived from Ottawa offering Clarrie an opportunity to join the Botany Unit's Weed Survey program, working with the venerable Herb Groh who constituted a direct link to James Fletcher, John Macoun, and other Victorian pioneers of Canadian field botany (Taschereau 1972a). They jointly prepared two editions of the Canadian Weed Survey in the late 1940s (Appendix 1). After Groh retired in 1948, Clarrie headed up and maintained the Weed Unit into the 1960s (Cody et al., 1986).

When he arrived at the Botany Unit's main building in Ottawa, Clarrie asked the first person he saw for directions to Senn's office. The helpful guide was botanical technician Enid Patterson with whom he would be married less than two years later. Although she retired when they were married (this was the post-war, late 1940s!) Enid remained keenly involved in natural history investigations. She applied her botanical training and personal interest with particular success after Clarrie retired, the two forming an unsurpassed team of floristic investigators in eastern Ontario and western Quebec.

Although attending to a broad sweep of floristic and taxonomic studies, Clarrie's professional focus began and remained with agriculturally troublesome weeds and their associated species. His field and herbarium expertise provided early identification of a number of previously unrecognized but now at least regionally significant weeds such as *Erysimum hieraciifolium* and *Salsola collina*. Clarrie is probably most widely known, however, for his authorship of *Weeds of Canada* which served as a major source of information on these economically important plants for decades. Later versions of this standard work were revised with Agriculture Canada colleague Gerry Mulligan. With Ray Moore, Clarrie also co-authored an authoritative book on the thistles of Canada (Appendix 1).

In a career spanning 1946 through 1970 with the botanical research group at the Central Experimental Farm (officially known as The Botany Unit, The Botany Division and the Plant Research Institute at various times but always referred to by researchers and regular visitors alike as "The Farm"), Clarrie held a variety of official positions. These included Chief of the Weed Investigation Section, Chief of the Taxonomy and Economic Botany Section, Associate Director of the Institute and for a two-year period, Acting Director of the Institute (Steeves 1973).

During this time he conducted a wide variety of research into various economic weed questions, working with a diversity of associates such as Herb Groh, Gerry Mulligan, John Bassett, Jim Calder and Bernard Boivin. His co-operative and generous nature and keen interest made him a much appreciated research collaborator

Clarrie and Enid Frankton, following Clarrie's receipt of 1986 Anne Hanes Natural History Award (April 1987)

who was known to bring rare and unusual skills to bear to the problems at hand. In the late 1950s and early 1960s, for example, he taught himself sufficient scientific Russian to satisfactorily translate appropriate sections of the mammoth *Flora of the USSR* as various volumes appeared, both for his own research purposes and for the benefit of his associates at The Farm.

Clarrie became an internationally recognized authority on many species of the economically important genera *Cirsium*, *Carduus*, *Atriplex*, *Rumex* and *Polygonum* (*sensu lato*). In collaboration with several associates (Appendix 1), Clarrie recognized many previously undetected taxonomic relationships and made significant improvements to the classification of taxa within these genera through the application of cytological data from Canadian specimens.

During this 25-year professional career Clarrie also developed a huge and loyal network of contacts and correspondents throughout Canada and beyond, including agricultural representatives, taxonomists and weed specialists. Although he traveled rarely, his network of contacts served him well. In addition to his professional associates at The Farm, his correspondents contributed much of the living and preserved plant material he required for his various investigations.

It is fair to say that Clarrie was a true scholar, one who valued the intellectual challenge of scholarship for its own sake and one who also cared deeply about its consequences. His natural sciences research was no ivory tower occupation. Much of his definitive work on weed species was of direct economic value to thousands of Canadian farm families and to the agricultural economy.

Although a prolific collaborator, he only relatively infrequently initiated publications (Appendix 1). Clarrie was perfectly content to leave it to associates and partners to incorporate his data and analysis within their work. Had he not been a taxonomist, however, he most certainly could have been a technical editor. He had an incredibly sharp eye for typographical

errors, factual inconsistencies and structural problems in the most complex and convoluted technical writing. He was particularly alert – no, *eager* – to point out spelling errors. Most of the scientific journal papers submitted from the botanical research group during his years at The Farm benefited greatly from his input. Many of those contributions to staff manuscripts were deemed worthy of co-authorship but Clarrie consistently refused, stating modestly that he was just doing his duty (C. Crompton, personal communication). The substantial impact and importance of his scholarship is expressed by appreciative associates through their appellation of such taxa as *Atriplex franktonii, Polygonum franktonii* and *Cirsium undulatum* var. *franktonis* (Taschereau (1972a), Wolf and McNeill (1986) and Boivin (1972), respectively).

While he was a member of and often active within many professional and non-professional organizations including the Canadian Botanical Association, The Ottawa Field-Naturalists' Club, Nature Saskatchewan, etc., he rarely served in official capacities. It should be noted, however, that he distinguished himself during two exceptions to this rule, in both cases remedying major organizational problems. As Ottawa Field-Naturalists' Club Treasurer (1947 – 1948) he undertook to sort out the disarray in Club finances which had arisen in large measure by sloppy attention to *Canadian Field-Naturalist* back-issue and reprint orders – a major source of revenues in those days. He and *Canadian Field-Naturalist* Business Manager Bill Cody worked mightily re-organizing the orders, many of which had been ignored for months and even years by a distracted editor, salvaging many of the invoices and thus generating a significant and sudden influx of revenue. That income became the investment foundation upon which the substantial equity which the organization presently enjoys was built. The situation was made all the trickier by the fact that the "distracted editor" in question was none other than their supervisor, Harold Senn!

Later, Clarrie served as Secretary-General of the 9th International Botanical Congress held in Montreal in August 1959. Called into the position only in late 1958, he used his organizational expertise to clear up serious logistical and organizational difficulties and ensure the successful achievement of the Congress programs.

In recognition of his years of scientific contributions he received the George Lawson Medal (lifetime achievement award) of the Canadian Botanical Association in 1973 (Steeves 1973). He was made an Honorary Member of the Ottawa Field-Naturalists' Club in 1980 (Brunton 1981), of which he was a member for 54 years. He had been considered for the Honorary Membership years before, largely in recognition of his critical role in organizing the 1959 Montreal International Botanical Congress. It was correctly felt at the time, however, that there would be plenty of other reasons, both local and national in scope, to recognize him with this honour in later years (1961 Awards Committee notes, Ottawa Field-Naturalists' Club collection, Public Archives of Canada).

Clarrie also served as advisor on agricultural science and botanical research matters to the Royal Commission on Government Organization (the 1962 Glassco Commission) which led to substantial re-organization of the way federal government departments were organized and operated. His efforts in this difficult and at times frustrating task were reportedly greatly appreciated both by Commission members and the agricultural research community (C. Crompton, personal communication).

Throughout all this, Clarrie was very active in floristic investigations in the National Capital Region, particularly so after he retired in 1970. He focused especially on a number of the most ecologically significant areas within the vast National Capital Greenbelt which surrounds the urban core of Ottawa. Here and elsewhere he and Enid discovered literally dozens of new records of regionally and provincially significant vascular plant records. Significant native rarities they discovered as new in the Ottawa District include the provincially significant *Huperzia selago* and *Woodsia oregana* ssp. *cathcartiana*, and the regionally significant (*viz.*, rare within the City of Ottawa (former Region of Ottawa-Carleton)) *Asplenium platyneuron, Spiranthes casei, Claytonia virginica, Polygala verticillata, Viola rostrata* and *Bidens discoideus* (Brunton 1998). And to this can be added many more first records for weedy species. This is a particularly impressive achievement in that the Ottawa District (the area within a 50 km radius of the Parliament Buildings in Ottawa) must surely be one of the most thoroughly botanized localities in Canada. Such lasting contributions as these were acknowledged in his 80th year when the Ottawa Field-Naturalists awarded him the 1986 Anne Hanes Natural History Award "*for outstanding contributions to the study of natural history of the Ottawa Valley*".

Clarrie's field explorations have also proven to be of critical importance to conservation efforts in the National Capital Region. Only months after his death, a magnificent, 250 ha-block of provincially significant forest, pond and rock barren landscape in the South March Highlands of Kanata (now within the City of Ottawa) was formally designated a natural environment reserve by the municipality. The major ecological rationale for this important, $1.6 million public conservation initiative was substantially formed by Clarrie's definitive field investigations.

Beyond all that, though, Clarrie's greatest contribution may have been his ability to inspire others. He was very much one of that band of post-war Canadian natural scientists including the late Earl Godfrey, George Ledingham, Bill Dore, Bernard Boivin and Bill Baldwin whose passion for their work – their calling, really – was readily transferred to others.

Clarrie shared with them a love of scholarship and was thrilled by the discovery process itself. And like those other noted scientists, he both respected and encouraged anyone involved in it, be they high powered professionals or concerned citizens. More than a few research scientists and ecological specialists, including Gerry Mulligan, former Director of the Agriculture Canada Biosystematics Research Institute, botanists Pierre Taschereau, and Cliff Crompton, entomologist J. Donald Lafontaine and this writer, have been proud to acknowledge the importance of Clarrie's encouragement and guidance in the development of major aspects of their professional careers.

Although pleased by the praise and honours of his peers, Clarrie might well have most appreciated being recognized as a true "amateur", one who undertakes an activity for the sheer love of it. He was *always* looking forward to new inquiries to be undertaken, new questions to be answered. Indeed, in his 95th year he remained as he had been for almost four decades, the "youngest" man I knew. His is a difficult though inspirational act to follow, but of that challenge I am sure Clarrie would simply have said, *"there you have it"*.

Well ... quite so.

Acknowledgments

Enid Frankton and Gwen provided important details on Clarrie's early years and family background and granted permission for the use of the photographic portrait from his athletic years. Bill Cody contributed a number of additions to the list of publications and Gerry Mulligan, Cliff Crompton, Carmen and Madeline Patterson, Karen McIntosh and Vic Sims shared valuable anecdotes, memories and perspectives on this remarkable individual. Important contributions were also provided by the thoughtful reviews of an earlier draft of this manuscript by Jacques Cayouette, Paul Catling and especially Cliff Crompton, former associates of Clarrie's at The Farm.

Literature Cited

Boivin, B. 1972. Flora of the Prairie Provinces Part III. Provancheria 4 Quebec. Pages 1-224.

Brunton, D. F. 1981. New Honorary Members of the Ottawa Field-Naturalists' Club. Canadian Field-Naturalist 95: 478-80.

Brunton, D. F. 1998. Distributionally significant vascular plants of the Region of Ottawa-Carleton. Planning and Development Approvals Department Report #28-09, Regional Municipality of Ottawa-Carleton, Ottawa.

Cody, W. J. 1997. A Tribute to Harold Archie Senn, 1912 – 1997. Canadian Field-Naturalist 111: 671-675.

Cody, W. J., D. B. O. Savile, and **M. J. Sarazin.** 1986. Systematics in Agriculture Canada at Ottawa 1886 – 1986. Agriculture Canada Historical Series Number 28, Ottawa.

Small, E., J. Cayouette., B. Brookes, and **W. Wojtas.** 1995. Canadian Biodiversity: a Guide to Botanical Specialists and Literature. Agriculture and Agri-Food Canada, Research Branch, Central Experimental Farm, Biological Resources Division, Ottawa.

Steeves, T. A. 1973. Presentation of Lawson Medals by the President of the CBA/ABC.The Canadian Botanical Association Bulletin 6 (3): 4-6.

Taschereau, P. 1972a. In memoriam: Herbert Groh. Canadian Field-Naturalist 86: 299-306.

Taschereau, P. 1972b. Taxonomy and distribution of *Atriplex* species in Nova Scotia Canadian Journal of Botany 50: 1571-1574.

Wolf, S. J., and **J. McNeill**. 1986. Synopsis and achene morphology of *Polygonum* Section *Polygonum* (Polygonaceae) in Canada. Rhodora 88: 457-479.

Received 1 December 2002
Accepted 31 October 2003

Appendix 1: Chronological bibliography of Clarence Frankton

[adapted from Small et al., (1995), with additions provided by W. J. Cody]

Frankton, C., and **L. C. Raymond**. 1941. An ecological and crop survey of Stanstead County. Macdonald College Pasture Studies XX. Scientific Agriculture 22: 178-194.

Frankton, C., and **L. C. Raymond** 1944. Pasture succession in the Eastern Townships of Quebec. Macdonald College Pasture Studies XXV. Scientific Agriculture 24: 271-281.

Frankton, C. 1948. Review of: Campagna, "Le problème de l'Herbe à Poux *(Ambrosia artemisiifolia)* (*Ambrosia trifida*), en Gaspésie." Canadian Field-Naturalist 62: 166.

Frankton, C. 1948. Review of: "1946 Annual report of the Provancher Society of Natural History." Canadian Field-Naturalist 62: 166.

Frankton, C. 1948. Review of: Florence Page Jacques, "Canadian Spring." Canadian Field-Naturalist 62: 166.

Groh, H., and **C. Frankton**. 1948. Canadian weed survey, fifth report, 1946. Canada Department of Agriculture, Ottawa. 86 pages.

Frankton, C. 1949. Review of: 1947 Annual report of the Provancher Society of Natural History. Canadian Field-Naturalist 63: 214.

Groh, H., and **C. Frankton.** 1949. Weed surveys in Canada. Agricultural Institute Review 4: 150-152.

Groh, H., and **C. Frankton.** 1949. Canadian weed survey, sixth report, 1947. Canada Department of Agriculture, Ottawa. 25 pages.

Groh, H., and **C. Frankton.** 1949. Canadian weed survey, seventh report, 1948. Canada Department of Agriculture, Ottawa. 144 pages.

Frankton, C., I. J. Bassett, and **F. Forsyth**. 1949. Comparison by bio-assay tests of 2,4-D esters of high surface activity with 2,4-D formulations now in use. Pages 76-77 *in* Proceedings of the 2nd meeting, Eastern Section, National Weed Commission.

Frankton, C. 1950. Review of: South Nation Valley Interim Report, 1948. Canadian Field-Naturalist 64: 190.

Bassett, I. J., and **C. Frankton.** 1952. Canadian havens from hay fever. Canadian Government Travel Bureau, Northern Affairs and National Resources. 30 pages. [2nd edition – 1955; 3rd edition – 1957; 4th edition – 1958; 5th edition – 1960; 6th edition – 1962.]

Frankton. C. 1954. A new weed, *Erysimum hieraciifolium* L. in Canada. Canadian Field-Naturalist 68: 27- 28.

Moore, R. J., and **C. Frankton.** 1954. Cytotaxonomy of three species of *Centaurea* adventive in Canada. Canadian Journal of Botany 32: 182-186.

Mulligan, G. A., and **C. Frankton.** 1954. The plumeless thistles (*Carduus* ssp.) in Canada. Canadian Field-Naturalist 68: 31-36.

Frankton, C., and **R. J. Moore.** 1961. Cytotaxonomy, phylogeny, and Canadian distribution of *Cirsium undulatum* and *Cirsium flodmanii*. Canadian Journal of Botany 39: 21-33.

Moore, R. J., and **C. Frankton**. 1962. Cytotaxonomic studies in the tribe Cynareae (Compositae). Canadian Journal of Botany 40: 282-293.

Moore, R. J., and **C. Frankton**. 1962. Cytotaxonomy and Canadian distribution of *Cirsium edule* and *Cirsium brevistylum*. Canadian Journal of Botany 40: 1187-1196.

Mulligan, G. A., and **C. Frankton**. 1962. Taxonomy of the genus *Cardaria* with particular reference to the species introduced into North America. Canadian Journal of Botany 40: 1411-1425.

Bassett, I. J., G. A. Mulligan, and **C. Frankton**. 1962. Poverty weed, *Iva axillaris*, in Canada and the United States. Canadian Journal of Botany 40: 1243-1249.

Selleck, G. W., R. T. Coupland, and **C. Frankton**. 1962. Leafy spurge in Saskatchewan. Ecological Monographs 32: 1-29.

Frankton. C., and **R. J. Moore**. 1963. Cytotaxonomy of *Cirsium muticum, Cirsium discolor*, and *Cirsium altissimum*. Canadian Journal of Botany 41: 74-84.

Frankton, C., and **R. J. Moore**. 1963. Cytotaxonomic notes on some *Cirsium* species of the Western United States. Canadian Journal of Botany 41: 1554-1567.

Moore, R. J., and **C. Frankton**. 1964. A clarification of *Cirsium foliosum* and *Cirsium drummondii*. Canadian Journal of Botany 42: 452-461.

Moore, R. J., and **C. Frankton**. 1965. Cytotaxonomy of *Cirsium hookerianum* and related species. Canadian Journal of Botany 43: 597-613.

Moore, R. J., and **C. Frankton**. 1966. An evaluation of the status of *Cirsium pumilum* and *Cirsium hillii*. Canadian Journal of Botany 44: 581-595.

Moore, R. J., and **C. Frankton**. 1967. Cytotaxonomy of foliose thistles (*Cirsium* spp. aff. *C. foliosum*) of western North America. Canadian Journal of Botany 45: 1733-1749.

Mulligan, G. A., and **C. Frankton**. 1967. Present status of tall wormseed mustard, *Erysimum hieraciifolium* in Canada. Canadian Journal of Botany 45: 755-756.

Frankton, C., and **I. J. Bassett**. 1968. The genus *Atriplex* (Chenopodiaceae) in Canada. I. Three introduced species: *A. heterosperma, A. oblongifolia* and *A. hortensis*. Canadian Journal of Botany 46: 1309-1313.

Moore, R. J., and **C. Frankton**. 1969. *Euphorbia* × *pseudo-esula* (*E. cyparissias* x *E. esula*) in Canada. Canadian Field-Naturalist 83: 243-246.

Moore, R. J., and **C. Frankton** 1969. Cytotaxonomy of some *Cirsium* species of the eastern United States, with a key to eastern species. Canadian Journal of Botany 47: 1257-1275.

Frankton, C., and **I. J. Bassett**. 1970. The genus *Atriplex* (Chenopodiaceae) in Canada. II. Four native western annuals: *A. argentea, A. truncata, A. powellii* and *A. dioica*. Canadian Journal of Botany 48: 981-989.

C. Frankton, and **G. A. Mulligan**. 1970. Weeds of Canada. Canada Department of Agriculture Publication 968. 217 pages.

Cody, W. J., and **C. Frankton**. 1971. Ragged robin, *Lychnis flos-cuculi* L. (Caryophyllaceae) in Canada. Canadian Field-Naturalist 85: 256-257.

Frankton, C. 1972. Review of: Carl Bode, "The best of Thoreau's Journals." Canadian Field-Naturalist 86: 110.

Mulligan, G. A., and **C. Frankton**. 1972. Chromosome races in *Rumex arcticus* (Polygonaceae). Canadian Journal of Botany 50: 378-380.

Moore, R. J., and **C. Frankton**. 1974. The *Cirsium arizonicum* complex of the southwestern United States. Canadian Journal of Botany 52: 543-551.

Moore, R. J., and **C. Frankton** 1974. The thistles of Canada. Research Branch, Canada Department of Agriculture, Monograph Number 10. 112 pages.

Bassett, I. J., C. W. Crompton, and **C. Frankton**. 1976. Canadian havens from hay fever (revised). Agriculture Canada Publication 1570. 21 pages.

Frankton, C., and **G. A. Mulligan**. 1987. Weeds of Canada (revised edition). NC Press Ltd., Toronto. 217 pages.

Frankton, C., and **G. A. Mulligan**. 1988. Les plantes nuisibles du Canada (revisée). Marcel Broquet Inc., Montréal. 218 pages.

Book Reviews

ZOOLOGY

Ontario Odonata. Volume 3 (including observations for the year 2001)

Edited and compiled by Paul M. Catling, Colin D. Jones and Paul Pratt. 2002. The Toronto Entomologists' Association, Toronto, Canada.

The third volume (208 pages) on Odonata (the order that includes dragonflies and damselflies) of Ontario is now available. About 25 papers are included, treating new Ontario records, notes on Odonata species rarely captured, changes in distribution patterns, annotated lists of Odonata from a region, characterization of species commonly confused, book reviews, an up-to-date checklist of 166 species (80% of the Canadian fauna!) and changes in abundance for many species since Walker's work in the 1940s, and a checklist of species.

The lists of Ontario records are most impressive, comprising about 62% of Volume 3, and summarizing in a database format the information about species, locality, number of males, females and immatures for each record. Though the bulk of the records are for 2001, additional records not previously published cover the years 1996 to 1998. The total number for these four years is an impressive 6059 records. Including similar lists in volumes 1 and 2, 15370 records are now databased for 1996 to 2001. Specimens in collections previously added to about 13000 Ontario specimens. This is an exceptional contribution to the natural history of Ontario, providing a solid base to show the distribution of each species, and for the conservation of Ontario Odonata. Hopefully in time, this information could lead to books on Odonata of Ontario. About 1800 databased specimens of Odonata of Ontario are deposited as voucher in the Canadian National Collection, which has been massively upgraded in the past two years (Figure 1).

FIGURE 1. Portion of the Odonata collection at the Canadian National Collection of insects. Unmounted specimens are filed in glassine envelopes.

Among the many articles, the one by Paul Catling on the characterization of males and females of *Lestes disjunctus* and *L. forcipatus* was most welcome. Both species have often been confused by many students.

The editors intend to produce this type of document for another two years. By then it is hope that about 25000 records will have been entered. These records will become the base for future work on Odonata of Ontario as well as a time capsule at the very end of the 20th and beginning of the 21st century. We must congratulate the 31 contributors listed with their address and e-mail coordinates on page 105. Such a massive effort could not be done singly.

To purchase copies of the 2000, 2001 and 2002 documents, contact Alan J. Hanks, 34 Seaton Drive, Aurora, Ontario, Canada L4G 2K1; Phone: (905) 727-6993, e-mail:A.Hanks@aci.on.ca

RAYMOND HUTCHINSON and HENRI GOULET

K. W. Neatby Building, 960 Carling Avenue, Ottawa, Ontario K1A 0C6 Canada

Mammals of Ontario

By Tamara Eder. 2002. Lone Pine Publishing, Edmonton, Alberta. 215 pages. $24.95.

Surprisingly, this is the first field guide to the mammals of Ontario published since Cross and Dymond's (1929) descriptive handbook. Although Dobbyn (1994) recently wrote a technical atlas of mammal distributions, the need for an identification book was probably lessened by the authoritative work of Peterson (1966) for the mammals of eastern Canada. Expectations were therefore high for the first guide written about Ontario mammals.

The book is beautifully presented with nice colour figures, good layout design, and relatively compact size. It begins with a colour-coded and page-referenced table of contents, which is also reproduced on the back cover. This is followed by an expanded quick reference guide to the 78 species of mammals, grouped by taxonomic order, found in Ontario. Eight species are excluded because they are essentially considered non-

resident or exotics in the province (Dobbyn 1994). There is a short introduction that discusses the major habitat types in Ontario, seasonal effects, and mammal watching in the province. Oddly, a map with 12 places to see mammals in Ontario is found 8 pages before the descriptions of some of these Provincial and National Parks. From a practical point of view, only a few of these parks (e.g., Algonquin) are readily accessible whereas others are essentially inaccessible (e.g., Polar Bear). It would have been useful to list some sites in southern Ontario, such as the Bruce Trail along the Niagara Escarpment. The introduction ends with an "About This Book" section going over the taxonomic organization, use of scientific and common names, distribution maps, and the identification of species. It does not, however, review the information or topics presented within each species account.

In general, topics covered in the species accounts include anecdotal natural history facts, other names in addition to the scientific and common name, description of the mammal, its range, habitat, and food; where it sleeps, number of young, and a description of similar species. These topics are interspersed with a combination of distribution map, illustrations, tracks, range of measurements, "Did you know?" sidebar, and usually a photograph. The maps, unfortunately, are difficult to read because the dark shading for presence and light shading for absence is confusing when overlaid on the base map, which is further shaded (with perhaps vegetation?). Occurring several times throughout the book is a duplication of information in the "Did you know?" section and also in the text. In addition, the illustration of a similar species is a reduced version from the original species account. The drawings and photographs are, however, of very good quality.

The species accounts are organized taxonomically by order and family with a brief introduction to each group. Some information in these introductions is unclear and there are no references cited in the text nor is there a bibliography presented at the end of the book to verify any facts. For example, in the carnivore section, skunks are placed in their own family separate from weasels based on recent DNA studies. However, it is also stated that hair seals share a common ancestor with weasels, which is misleading because walruses and skunks are each more closely related to hair seals and weasels, respectively, as was also concluded by the same DNA studies (Dragoo and Honeycutt 1997). The bat and shrew sections each begin with a dichotomous identification key to species, which seems unexpected because none of the other groups has one. The species accounts, which comprise 85% of the book, are followed by a short glossary and indices to scientific and common names.

My major complaint about this book is that most of the information has been previously published in other mammal field guides by Lone Pine Publishing. This includes sections copied verbatim, in addition to the use of the same photographs and illustrations for species that happen to be found in both areas of interest. This style of "form-letter" field guides leaves very little specific information about the animals in Ontario. There is only generalized information about the species in North America as evidenced by the range descriptions with no details about where the mammal is found in Ontario. Nonetheless, the book presentation is good, although I would have preferred an expanded introduction going deeper into issues such as the role of mammals in the environment and conservation of biodiversity in Ontario. If you already have a book in this series, it may not be absolutely necessary to get another, but one is definitely nice.

Literature Cited

Cross, E. C., and **J. R. Dymond**. 1929. The mammals of Ontario. Royal Ontario Museum of Zoology, Handbook Number 1, University of Toronto Press.

Dobbyn, J. S. 1994. Atlas of the mammals of Ontario. Federation of Ontario Naturalists, Don Mills, Ontario.

Dragoo, J. W., and **R. L. Honeycutt**. 1997. Systematics of mustelid-like carnivores. Journal of Mammalogy 78: 426-443.

Peterson, R. L. 1966. The mammals of eastern Canada. Oxford University Press, Toronto.

BURTON K. LIM

Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6 Canada

Mammals of North America

By Roland W. Kays and Don E. Wilson. 2002. Princeton University Press, Princeton. 240 pages, Cloth U.S. $19.95

This new field guide is just what a field guide should be, small, well-organized and informative. Princeton has adopted the best format of having the animals' illustrations on the right page of each two-page spread, while on the left is the text and distribution map. I've never liked the other formats where the reader must go to up to three different parts of the same guide for these obviously-related pieces of information.

This guide also has several two-page spreads that perhaps were based on the great examples in the *Golden Guide to Birds of North America*. In the latter, all of the confusing warblers, and then all of the sparrows, are illustrated a second time on two-page spreads to help the field biologist or birder more quickly identify these tricky birds. In the Princeton guide, the "confusing cave Chiroptera" are so illustrated, as are bow-riding whales and dolphins. Further double-page illustration sets are in black-and-white, and include profiles of breaching and blowing whales, scats, and foot prints. I like these; in the field, these two-page spreads are a joy to use and save much page-flipping.

The illustrations have been created by eleven artists, and as a general comment, I think they are all good.

To my eye, the mice and vole illustrations are just a bit too cute, and the carnivores look like they've been drawn from mounted specimens…they're somewhat stiff in appearance. With some of the particularly difficult species, illustrations of some bony material accompanies the main image; the opportunity to use this information would likely be restricted to taxonomists or biologists studying carnivore diets. I question the value of, for instance, including chipmunk genital bones in a field guide. This type of material is more apt for specialty publications.

There are a few editorial problems that appear. I found the maps too small and they do not contain the boundary that distinguishes Nunavut from the Northwest Territories. The very odd *Aplodontia rufa* is listed with the common name of Sewellel; the older name of Mountain Beaver is not mentioned, which makes their statement, "Poorly named, this primitive rodent is neither aquatic nor fond of mountains…" seem rather out of place. The Gaspé Shrew range is incomplete, as it is known to occur in Nova Scotia as well. *Pappogeomys* is listed in the introduction to a plate, but no such genus is mentioned further on, *Cratogeomys* is used instead. Although the taxonomy of these pocket gophers is in turmoil, this book should have adopted one genus or the other for these rodents.

Overall, this is a very good field guide; with the editorial glitches cleaned up in a second edition, this will be a great field guide.

RANDY LAUFF

Department of Biology, St. Francis Xavier University, Antigonish, Nova Scotia B2G 2W5 Canada

The Complete Guide to Antarctic Wildlife

By Hadoram Shirihai. 2003. Princeton University Press, Princeton and Oxford. 510 pages. U.S. $49.50.

The ecotraveller to the southern ocean will rejoice at having a single book that covers all the normally occurring birds and mammals of that region. Indeed, this book is much more than a simple field guide. It starts with a synopsis of the region and it ends with detailed descriptions of the major locations of interest, with the species accounts sandwiched in between. This additional material occupies a third of the book, so it contains a substantial amount of information. Included are accounts of geology, geography, habitats, human history and conservation. The regional descriptions explain where the key locations they are situated, what they are like and how to get there. They also explain the birds and mammals most likely to be found, with specific instructions for the difficult-to-locate species.

Ice is a major factor in the lives of all the region's inhabitants. Shirihai has written a handy little section on surface ice, its forms and formation and its features. It took me several weeks of research to collect similar information a few years ago. He does not mention the subsurface ice (which very few people see) that also has many profound effects (damping currents, shielding UV rays, scouring the sea bed, etc.).

The author also does a good job of explaining the ecology and history of the regions. The human history section is a scant seven pages, so it only skips the surface of many remarkable tales. But then this is not a history book.

The Species accounts are well organized and well written. There is a good description of each animal, with a notation about the possible species that could cause confusion in the field. The author also adds a short note on conservation, distribution and biology. A 7 × 7 cm range map accompanies most of the species accounts. To avoid the problems of defining the taxonomy of some difficult-to-resolve species, the author has treated all forms as species, while noting the alternative taxonomic ideas. This neatly sidesteps the issue for birds that may be split and means the book will not go out of date for a long time. It does make it more difficult to use the index as; for example, Yellow-nosed Albatross is entered as Indian Yellow-nosed and Atlantic Yellow-nose in the albatross section. (That is under I and A and not Y). It does less well for birds that have been lumped. For example; the author lists *Buteo polyosoma* as Red-backed Hawk. This has been lumped in the more recent texts with Puna Hawk as Variable Hawk (*Buteo poecilochrous*), so you have to know the alternative, older taxonomy when using the index.

A good example of a species account is the one for Black-browed Albatross. The descriptions are clear and accurate covering adult, juvenile and two ages of immature. There is a description of voice and biometrics. The note on similar forms includes the Campbell Albatross, a split of the tiny Campbell Island population. Apart from the plate containing three depictions there are five photographs – three different ages in flight, a pair displaying and an adult with a fuzzy chick (there are two other photographs in the section on the Falkland Islands). There is a short account of the biology and an accurate current account of the serious conservation issue facing this graceful bird.

There is only one English name given for each species. Those not used to scientific names may have some confusion where the names vary from earlier texts. Many older texts refer to the Pale-faced and Black-faced Sheathbill as American (or Greater) and Lesser Sheathbill, respectively. There is also a poetic and historical loss too. The Striated Caracara is widely, affectionately and historically known as "Johnny Rook." In addition, the author continues to use some of the old English names such as Light-mantled Sooty Albatross over the newer and simpler Light-mantled Albatross.

The species accounts contain plates by Brett Jarrett. These are extremely well done. They are as good as the very best of Roger Tory Peterson's work. I did wonder briefly about the accuracy of the South Polar Skua painting, but quickly remembered I have a photograph of several of these skuas that show a range of plumage colours. This level of excellence is carried through the birds, seals and whales.

In addition, there are at least two photographs per page, occupying a quarter to a third of the space. With a few exceptions the quality of these photographs is stupendous. Not only are they good portraits of the individual species, but also they frequently capture an insight above and beyond a mere representation. These photographs were taken by a large number of photographers, although a good proportion is by Shirihai himself. Sadly the only members of the beaked/toothed whale group with photographs are Blainville's and Cuvier's Beaked Whales – a testament to how elusive these creatures are.

I work in a domain where the meaning of each word is important and is often argued over for long periods. So I was taken aback by the book's formal title: *The Complete Guide to Antarctic Wildlife*. It is not complete nor does it deal with all wildlife, for it only covers two classes from one kingdom. Although many members of other kingdoms are mentioned in the text there are only species accounts for birds and marine mammals. The index lists the mammals and birds only. The book is not confined to the Antarctic but includes New Zealand, Southern Australia, Southern Africa and South America. The books subtitle is "Birds and Marine Mammals of the Antarctic Continent and the Southern Ocean", which is much more accurate. The second title would better justify Sirihai leaving out the region's land mammals (rats and reindeer for example).

There are some other odd errors in this book. The index has six of the plates mixed up and some of the non-bird-marine mammal wildlife is not included. The first figure, a map of the entire region covered, has the island of South Georgia about 3 degrees too far east.

I was a surprised to see the geographic distribution of the Sub-Antarctic Fur Seal included Macquarie Island, off New Zealand. This species' normal range is the Atlantic and Indian Oceans off South Africa. But the text revealed that this mammal has recently become established on Macquarie – a long, but not impossible voyage for a seal.

If you plan to visit the southern oceans then this is the best single, portable book for you to take. Although be warned, this book weighs about twice as much as books of a similar size, as it has very high quality silky paper (that has a wonderful feel). Once you are in your cabin (the only way to visit these islands is by ship), then you can ignore the weight and enjoy the astounding quality.

ROY JOHN

2193 Emard Crescent, Beacon Hill North, Ottawa, Ontario K1J 6K5 Canada

Reptiles and Amphibians of Algonquin Provincial Park

By Ronald J. Brooks, Dan Strickland, and Russell J. Rutter. 2003. The Friends of Algonquin Park, P.O. Box 248, Whitney, Ontario. 49 pages. $2.95.

The first edition of *The Reptiles and Amphibians of Algonquin Park* was published in 1976, authored by Dan Strickland and Russell J. Rutter, long-time naturalists at Algonquin. Its success led to revision and reprinting in 1978, 1986, and further reprintings in 1992 and 2000. The 2003 edition is 48 pages, magazine format (29.7 × 21.0 cm), with tightly-packed text featuring extensive new portions by Ronald J. Brooks, University of Guelph. The latter are for the turtles, all snakes except the Common Gartersnake, and most of the Yellow-spotted Salamander, Green Frog, Mink Frog, and Bullfrog accounts. All of these species, save the snakes, have been focused on in the intensive research of Brooks and his many graduate students in Algonquin Park over three decades. Their enthusiasm for promoting increased awareness of the place of, and threats to, amphibians and reptiles is palatable throughout.

An introductory section defines amphibians and reptiles and the problems of being "cold-blooded" and discusses environmental, behavioural, and physiological adaptations such as "How to Beat the Cold Underwater" and "How to beat the Cold on Land". Species accounts are grouped and these are prefaced by introductory material. Accounts deal briefly with recognition and distribution within the park but the bulk of the text of each is graphic and vivid word pictures of life history and behaviour.

A typical example of Brooks' distinctive style, from the Snapping Turtle account, concerns the difficulties of saving individuals which have wandered on highways. After advising avoidance of the jaws and claws, it continues with additional caution of supplementary defensive measures. "When upset, Snapping Turtles exude a foul-smelling liquid from the bridge between the carapace (top shell) and plastron (bottom shell). This liquid looks like maple syrup but is rather less delightful and imparts an odour that the researcher comes to associate with Algonquin. The rank smell of reptilian rage on one's hands will last 2 to 3 hours. But the bites, scratches and stench are all worth it when one sees the ungrateful recipient of one's compassion stagger awkwardly into a fetid bog, safe from the speeding giants of Highway 60."

Or the description of post egg-laying behaviour: "Slowly, the mother begins to pull earth back into the nest, carefully pressing it around the eggs. Each hind

foot reaches out to the side and the foot flexes and drags sand and pebbles into the hole. When the hole is partly full, the female braces on her front feet and tail to form a tripod, makes a 'fist' of her hind feet and swings side to side punching the earth tightly in the nest. This whole process can only be described as beautiful beyond words."

Interspersed among the species accounts are "sidebars" of general interest: "Are Turtles Immortal?", "More Park Roads Would Mean Less Protection for the Park's Threatened Wildlife", "Hidden Talents", "Getting launched in life", "Salamanders and the danger of acid rain", and "Are frogs and other amphibians declining in Algonquin Park".

An attractive visual feature of the publication is the 138 colour photographs. These illustrate adults of all 31 species (5 turtles, 9 snakes, 7 salamanders and 10 frogs, treefrogs and toad) covered by the text. As well, they include juveniles and eggs of most, some key features, and habitat and field workers in Algonquin Park. There are four maps of approximate northern range limits for various groups of reptiles and the number of days above 18°C (from 250 and more for the most southern group to 100 and less for the Common Garter Snake). Two line drawings illustrate snakes' belly scales, spilt (divided) and unsplit "cloacal" (anal) scales, and smooth and keeled scales. Ten mini-drawings depict representative species of the 10 families listed in the table of contents.

In contrast to the "cutting edge" information throughout most of the book, the account of the Blue-spotted Salamander complex has not been well updated; particularly noticeable is the omission of Canadian work of the last decade from University of Guelph (James Bogart) or the Royal Ontario Museum (Bob Murphy and Les Lowcock). Missed in the "Further Reading" section is *The Royal Ontario Museum Field Guide to Amphibians and Reptiles* by Ross MacCulloch (reviewed in *The Canadian Field-Naturalist* 116(4): 653-654), published in 2003 but prehaps not until after the Algonquin text had been prepared.

For any naturalist visiting Algonquin Park, this book is a must, but others, even if they will never go there but want to increase their appreciation and general knowledge of amphibian and reptile behaviour and adaptation, will find the text a joy to read cover to cover.

FRANCIS R. COOK

Canadian Museum of Nature, Ottawa, Ontario K1P 6P4 Canada

Herpetology in Montana: A History, Status Summary, Checklists, Dichotomous Keys, Accounts of Native, Potentially Native, and Exotic Species, and Indexed Bibliography

By Bryce A. Maxwell, J. Kirwin Werner, Paul Hendricks, and Dennis L. Faith. 2003. Society for Northwestern Vertebrate Zoology, Olympia, Washington, Northwest Fauna Number 5. viii + 138 pages.

This meticulously prepared analysis of state distribution and literature justifiably bills itself as "the most through compilation of information on Montana's herpetofauna to date". It covers 12 amphibian and 17 reptile species regarded as native in the state in individual species accounts as well as a review of 7 additional species or subspecies which are possibly native and 13 species or subspecies that have been reported as exotic.

An initial 10-page history of Montana herpetology is followed by a summary of information on, and status of, the herpetofauna. Seven figures present chronological summaries of voucher and observation records, of major contributions, of articles and percentage contribution by types of literature, the number of articles by species, and maps of number of amphibian and reptile species by county. Checklists for the native amphibia and reptilia are followed by keys to amphibian eggs, larvæ, and adults juveniles and to adult and juvenile reptiles.

A five-page introduction to the species accounts discusses the spot distribution maps (39 institutions provided information on 3396 amphibian and 1240 reptile voucher specimens and contained 3286 and 1163 mappable locality data, respectively; 4654 amphibian and 2349 reptile observations from a variety of sources were also mappable). After the fist mapping of this data base extralimital or otherwise questionable records were verified by contacting the museum or observer and a number of errors of identification were found, as well as some where verification was not possible because the museum specimens were now missing. The authors stress that anyone conducting primary research should confirm the interpretations of localities presented for museum voucher specimens by contacting the institutions directly.

The bulk of the text (pages 30 to 105) presents the species accounts which include a distribution map for each species with the total records on which the map is based, general comments, earliest records (literature and voucher specimen), maximum elevation voucher record, a voucher record summary by county, and a bibliographic index by topic. There is no field data, no descriptions (other than the keys) and no ecology or behaviour. The only illustrations are on the front (Western Rattlesnake) and back (neotenic Tiger Salamander and head views of Western Rattlesnakes) covers reproduced from the literature of the 19th century.

A notable exclusion from the verified species list (but included in the "potentially native" list) is *Bufo hemiophrys*, widespread over much of Alberta and Saskatchewan to the north. It was recorded only in the northeastern corner of the state by the late Jeffery Black in his surveys in the late 1960s and early 1970s and no

voucher specimens can now be found. Another Black Montana record, the Spotted Chorus Frog, *Pseudacris clarkii*, is here relegated to the "exotic species" list, as based on misidentification of green-spotted variants of the widespread and abundant Boreal Chorus Frog, *Pseudacris maculata*. This is certainly the correct interpretation as similarly patterned individuals are present in adjacent populations of Boreal Chorus Frogs in Alberta and Saskatchewan (FRC, personal observations).

A bibliographic index of amphibian/reptile guides for Montana and surrounding states and provinces has surprisingly omitted The British Columbia Museum Handbooks to amphibians by Carl first published in 1943, and by Green and Campbell in 1984 and to reptiles by Carl first published in 1944 and by Gregory and Campbell in 1984. Perhaps they are regarded as superseded by the more recent publications listed for American authors which include British Columbia. Canadian provincial guides to Alberta and Saskatchewan, however, are included. A bibliography includes 543 entries. A detailed form for reporting incidental observations and a map of Montana counties conclude the book.

The thoroughness of preparation and evaluation of records make this volume a notable contribution to the growing effort to produce detailed state atlases. When the records are as carefully evaluated as they are here, they have broad use, not just for conservationists and zoogeographers, but for keen field naturalists who want a base-line of information in order to evaluate their own past and future observations for potential significance.

FRANCIS R. COOK

Canadian Museum of Nature, Ottawa, Ontario K1P 6P4 Canada

Guide to the Reptiles of the Eastern Palearctic

By Nikolai N. Szczerbak. Technical Edit by Michael L. Golubev. 2003. Krieger Publishing Company, P. O. Box 9542, Melbourne, Florida 32902-9542, 250 pages. Cloth U.S. $73.50 ISBN 1-57524-004.1.

The text was originally prepared to cover the 22 million km^2 (11 million of which is affected by permafrost) of the Union of Soviet Socialist Republics but the subsequent breakup of that political entity necessitated retitling. As the former USSR encompassed much of Palearctic [Palaearctic of some texts] of zoogeographers, exclusive only of western Europe and southern Asia, the revised title in appropriate. The author, Nikolai N. Szcerbak (1927-1998) had excellent credentials as a long-time staff member of the zoological museum of the Ukrainian SSR Academy of Sciences Zoology Institute and, later, the Ukrainian Natural History Museum. He participated in almost 60 expeditions, visiting every area of the USSR, and authored or coauthored 24 monographs, 12 popular science books, and close to 300 scientific articles. From the title one expects a volumen equivalent to the 1999 *Amphibians of the Former Soviet Union* by S. L. Kuzmin (reviewed 2002 in *The Canadian Field-Naturalist* 116(4): 665-666) but much less detail is delivered here, not surprising in that over four times the number of reptiles are covered compared to the amphibians (165 vs 40).

There are only 11 pages of introductory general material and a herpetological overview of the eastern Palearctic and its subdivisions. The bulk of the text, 220 pages, is keys and species accounts. The latter give Distribution (for former USSR and extralimital), Natural History (including habitat, food, activity, fecundity, incubation or gestation, size at hatching or birth, age of maturity and maximum size), Status (abundance and if at risk), References and Remarks, the latter including taxonomic notes and subspecies recognition and range. There is an outline map of the former USSR for each species with the range indicated in black. The centre of the book has 194 adequate colour photographs depicting habitats (half page each) and species and subspecies (a third of a page each), the latter most often on natural backgrounds.

A total of 168 species (55 genera) are recognized for the region. Included are 7 species (5 genera) of turtles and tortoises; 98 (25) lizards; and 63 (25) snakes. This contrasts with 39 species (26 genera) of reptiles for Canada where there are 8 (7) [exclusive of marine and introduced species] turtles; 6 (3) lizards; 25 (16) snakes. The disproportionate numbers of snakes and lizards in the eastern Palaearctic is largely due to more extensive southern latitude arid areas included where a greater diversity of reptiles have evolved, as in the arid southwestern United States. All three turtle families represented have species in Canada, as do 3 of the 6 families of lizards and 3 of the 6 families of snakes. No species and few genera are common to Canada, only the large "catch-alls" of the latter, *Eumeces* for the lizards, and *Coluber* and *Elaphe* for snakes. For them, eventual revisions will likely distinguish a nearctic group from the palearctic one as already has been accepted for the turtles *Emydoidea* and *Emys*, and snakes *Nerodia* and *Natrix*.

The book concludes with a 13-page bibliography, including many papers in Russian [with translated titles], mostly from the 1980s and early 1990s, none later than 1996.

Overall this useful summary of knowledge of the northeastern Palearctic herpetofauna to the mid-1990s has much to stimulate the comparative zoogeographer and/or ecologist.

FRANCIS R. COOK

Canadian Museum of Nature, Ottawa, Ontario K1P 6P4 Canada

Herpetology: An Introductory Biology of Amphibians and Reptiles, Second Edition

By George R. Zug, Laurie J. Vitt, and Janalee P. Caldwell. 2001. Academic Press, A Harcourt Science and Technology Company, 525 B Street, Suite 1900, San Diego, California 9210-4495 USA. xiv + 630 pages.

This book can trace its origin back to the pioneering textbook *Introduction to Herpetology* by Coleman J. and Olive B. Goin published in 1962 (reviewed by J. S. Bleakney in *The Canadian Field-Naturalist* 77(3): 170-171), with a second edition in 1971 (reviewed in *The Canadian Field-Naturalist* 88(2): 248-249). A third edition in 1978 added George Zug as coauthor. In 1993 a completely new *Herpetology* by Zug appeared (reviewed in *The Canadian Field-Naturalist* 109(4): 483-485). Its present second edition is so extensively rewritten it could well be considered a new work itself. Not only has it increased in thickness by 103 pages, but it has more text per page, as it is broadened in height and width, from compact textbook 23.4 × 15.7 cm to near coffee-table format at 28.5 × 22.1 cm.

The bulk of the new text is in six parts covering 531 pages: (I) Evolutionary History — Tetrapod relationships and evolutionary systematics, anatomy of amphibians and reptiles, Evolution of ancient and modern amphibians and reptiles; (II) Reproduction and Life Histories — Modes of reproduction and parental care, Reproductive ecology and life histories; (III) Physiological Ecology — Water balance and gas exchange, Thermoregulation, performance, and energetics; (IV) Behavioral Ecology — Spacing, movements, and orientation, Communication and social behavior, Foraging ecology and diets, Defense and Escape; (V) Population and Community Ecology — Population structure and graphical ecology, Conservation biology; (VI) Classification and diversity — Caecilians, Salamanders, Frogs, Turtles, Crocodilians, Tuataras and Lizards, Snakes. These are followed by a 6-page Glossary of technical terms from "abiotic" to "xeric". The Bibliography covers 57 pages with the vast majority of entries being from the 1980s and 1990s. Two indices conclude the book, one to taxonomic names and the other to subject.

The authors (as outlined in the preface) have updated the text in line with contemporary (to mid-1999) systematic practices in biology. New phylogenetic concepts lead hierarchial reworkings of classification by clades, each "a group of organisms containing an ancestor and all its descendants". The latter led to major change that will seem especially radical to the lay reader. Traditional textbook higher-level labels such as order, class, etc., have been abandoned, and even family and subfamily categories have been avoided as such. However, names formerly applied to the latter are often retained for current clades. Throughout, one cladistic interpretation has been selected for each group, sometimes the result of combining two previously proposed. However, a strength of the presentation is its illustration of the dynamic, seemingly ever-changing, state of modern systematics by the frequent inclusion of alternate classifications of recent authors. Like the previous edition birds are shown as within the reptilia clade, paired with the crocodylians among the living groups (figure 1.15). For convenience, however, the text covers reptile biology only for the traditional unit exclusive of birds, still leaving the biology of feathered reptiles to textbooks by ornithologists.

Throughout the entire work references are given to the literature for all subject matter, either cited directly in the text for specific studies or at the end of each section under additional reading and reference headings. The book is profusely illustrated with black-and-white figures, diagrams, and photographs through the first five parts. But the sixth has colour, both for ranges in the many distribution maps and also for often spectacular photographs of living individuals representing significant clades.

My review of the 1993 edition concluded (quoted by the publishers on the back cover of the new edition), "This will be a valued, and oft-consulted, addition to any naturalists' or conservationists' library for its up-to-date comprehensive overview of these ecologically important groups and their role in the contemporary environment; it is a must for anyone just starting into the field of herpetology in order to orientate themselves." This is even more true now for the new edition which, sweepingly and effectively, largely replaces the old. However, conservatives in classification may still want to keep the earlier edition handy on their shelves for reference to traditional units of higher classification.

FRANCIS R. COOK

Canadian Museum of Nature, Ottawa, Ontario K1P 6P4 Canada

In Quest of Great Lakes Ice Age Vertebrates

By J. Alan Holman. 2001. Michigan State University Press, East Lansing, Michigan 48823-5202. ix + 230 pages.

J. Alan Holman has published four previous books, more than 240 papers, and numerous popular articles during a distinguished pursuit for evidence of Pleistocene vertebrates, particularly amphibians and reptiles (see review of his scholarly *Pleistocene Amphibians and Reptiles in North America*, 1997, reviewed in *The Canadian Field-Naturalist* 111(4): 696-697).

Here he aims at a more semi-popular approach in a near coffee-table large format (28.5 × 22.1 cm) narrowed geographically to concentrate on the Great Lakes but expanded taxonomically to encompass all vertebrates. An Introduction is followed by nine chapters: The Pleistocene Ice Age, The Pleistocene in the Great Lakes Region, Where to Find Vertebrate Fossils, Collecting the Fossils, Dating the Fossils, A Bestiary of the Great Lakes Region Ice Age Vertebrates, Important Pleistocene Vertebrate Sites in the Great Lakes Region, Interpretation of the Fauna, and The Holocene and the Aftermath of the Ice Ages. An eight-page appendix lists the occurrence of all species by subregion. The bibliography is 17 pages arranged by chapter. Finally, two pages give illustration credits, two a General Index, and four an Index to Common and Taxonomic Names.

Half the book, 114 pages, is taken up by the "Bestiary" which details the orders, families and species of fish, amphibians, reptiles, birds, and mammals that are recorded for Pleistocene fossil sites in Wisconsin, Illinois, Indiana, Michigan, Ohio and Ontario. Morphological and ecological characteristics are given from living animals when populations still are extant, and conjecture on the latter when only known from fossils. Sites are listed for each species and these are mapped for various groups. Drawings are provided of the majority of species and some diagnostic bones. The latter are exact, but the whole animal depictions are of variable quality. The mammals, though tending to be fuzzied or outlined only, are adequate, as are the turtles and the fish (the latter mostly outlines). But the token birds (ducks) are poor as is the anolis lizard (a southern species surprisingly included as representative of the group despite not occurring as fossil in the region covered). The full snake (a coachwhip) is crude – naked, appearing skinned — and the frogs are atrocious, apparently overlaid with fly-screening, particularly the supposed Green Frog.

The site-by-site chapter is 26 pages. Eight sites from Ontario are included ranging from early to late Wisconsin. The Rostock Mammoth Site in Perth County near Stratford in southern Ontario has provided a pollen record of vegetation correlated with radio-carbon dates to give an outline of ecological changes. From 14000 to 13000 the area was a wasteland very near the glacier, from 13000 to 12000 a tundra woodland, from 12000 to 10000 a boreal woodland.

Inevitably, an occasional lapsus occurs. One notable one is on page 182 in a discussion of the only Late Wisconsin reptile in the Michigan record, the Painted Turtle, *Chrysemys picta*. Although probably correctly considered to be "the most cold-tolerant turtle in North America" it is questionably characterized as having "the most northern distribution" (Snapping Turtles in central and eastern Canada and Wood Turtles in the east may at least stray as far or farther north). The statement seems based on erroneously crediting the Painted Turtle as "occurring north to the Great Slave Lake". The only reptile with this northern a range is the Red-sided Gartersnake, *Thamnophis sirtalis parietalis*. For the Painted Turtle, I know of documentation only north to 51° in Lake Winnipeg, Manitoba.

Holman sums up the remarkable wave of extinctions at the end of ice age (page 196) with: "Let us say that everything went wrong at once at the end of the Pleistocene. The climate changed from an equable one to a nonequable one, mating and birthing in large herbivores became out of step with the new climate, mosaic communities gave way rapidly to less diverse communities, large herbivores are thrown into intense competition with one another, and salt supplies for salt-dependant megahervivores diminish because of lower water tables. Humans and other mammals emigrating from Eurasia to North America bring new diseases to which the New World mammals lack immunity. Finally, for some unexplained reason, bands of experienced, intelligent hunters 'lose it' and kill every large mammal in sight as they move from Alaska to the tip of South America."

Finally, Holeman further adds "Biodiversity, which suffered a tremendous blow at the end of the Pleistocene and took another hit when monoculture agriculture replaced natural plant communities, continues to diminish in an almost out-of-control fashion, as natural communities are replaced helter-skelter by artificial human habitation". After observing that inevitably the present Holocene itself will be replaced by a new unit of geological time he finishes in an apparently up-beat fashion with a wish that the next epoch will be "marked by natural geological processes rather than by human-induced catastrophic extinction".

FRANCIS R. COOK

Canadian Museum of Nature, Ottawa, Ontario K1P 4P6 Canada

Snakes of the United States and Canada

By Carl H. Ernst and Evelyn M. Ernst. 2003. Smithsonian Books, Washington. xi+668 pages. US$70, CAN$105.00 ISBN 1-58834-019-8

It is over four-and-a-half decades since the publication of the comprehensive two-volume *Handbook of Snakes of United States and Canada* by Albert Hazen and Anna Allen Wright (reviewed in *The Canadian Field-Naturalist* 71(4): 201-202 by J. S. Bleakney, 1957). Those volumes emphasized the need for life history data and presented the first distribution maps for all species covered (this was a year before the first field guide to amphibians and reptiles in the Peterson series appeared). The intervening period has seen not only a proliferation of ecological and behavioural studies but the compilations of extensive data-bases on distribution for virtually every region of North America. In the new treatment of North American snakes, the Ernsts have synthesized much of the new information and integrated it with the historic data in detailed species accounts.

A seven-page Introduction begins with remarks on the taxonomic position snakes (over 2600 are recognized in the world) as a suborder (Serpentes) of the order Squamata which they share with lizards. Following are capsule sections on origins (the oldest fossil snake is from the early Cretaceous Period). The modern snake fauna (6 families, 52 genera and 131 species occur in North America), characteristics, habitat, activity periods, movements, reproduction, diet, predators and defense, venoms, populations, conservation. Two pages on identification include labelled diagrams of scale patterns and a key to the families.

The family and species accounts occupy 554 pages: Leptotyphlopidae (Slender Blindsnakes) 1 genus, 2 species; Typhlopidae (Blindsnakes) 1, 1 (introduced); Boidae (Boas) 2, 3 (one of these introduced); Colubridae (Colubrid Snakes – both harmless and rear-fanged species) 42, 105; Elapidae (Elapid Snakes – coral snakes and the marine Yellow-bellied Sea Snake) 3, 3; Viperidae (Viperid Snakes – represented by the subfamily Crotalinae, the pit vipers) 3, 17. Each account has sections on Recognition, Geographic Variations (including definition of all subspecies, some recognized as full species by other authors, and reference to forms once named but not currently recognized), Confusing Species, Karyotype, Fossil Record, Distribution (both as text and as a black patch on outline map of U.S. states, and, for the 25 species which range north of the U.S., the relevant portions of Canadian provinces), habitat, behavior, reproduction, growth and longevity, diet and feeding habits, predators and defense, populations (abundance), and remarks (additional aspects). Throughout the accounts sharp colour photographs illustrate each species and some distinctive subspecies.

The maps have surprisingly good detail despite their size which ruled out plotting individual records. The subdivisions of ranges into subspecies is not mapped but given only in the text. Distributions for the 25 species (three families) which range into Canada are generally accurate. Exceptions may be the central Saskatchewan, Alberta and British Columbia portions for the Western Terrestrial Gartersnake *Thamnophis elegans* (page 385) and the central Alberta and British Columbia portions for *Thamnophis sirtalis* (page 429) where, following some other recent authors, a disjunct patchwork is shown. These likely reflect just a lack of sufficient observations in these areas rather than actual range gaps. There is a northernmost disjunct shown for the Northwestern Garter Snake, *Thamnophis ordinoides* (page 403), apparently in the vicinity of Bella Coola. However, specimens identified as to this species in the literature are actually *Thamnophis elegans vagrans* (Canadian Museum of Nature, FRC unpublished data). A lapsus in paste-up has caused the map for the Common Garter Snake, *Thamnophis sirtalis* (page 429), to lose the portion for northern Alberta into the Northwest Territories at Fort Smith. This is unfortunate as it includes the most northerly record for a reptile in North America, documented as early as the beginning of the 20th century. However, this part of the range is included in the text. A discredited record for the Sharp-tailed Snake *Contia tenuis* (page 88) for the British Columbia interior continues to be plotted here. The northern limit of the Brown Snake *Storeria dekayi* is probably too generous in Quebec but the stylized boundaries of the map in this area make this hard to evaluate.

Some taxonomic details will be of interest to Canadian workers. The generic name *Liochlorophis* is accepted for the Smooth Green Snake (*L. vernalis*) but three previously named subspecies (*vernalis*, *blanchardi*, and *borealis*) are not. For the Plains Garter Snake (*Thamnophis radix*) the subspecies *haydeni* is no longer recognized. However, the subspecific status of the Blue Racer *Coluber constrictor foxii* for Great Lakes populations is considered valid, as are the two subspecies of Brown Snake (*Storeria dekayi*) that intergrade in Ontario and Quebec (*dekayi* × *wrightorum*). The Black Hills Red-bellied Snake (*Storeria occipitomaculata pahasapae*) is now regarded as intergrading with *S. o. occipitomaculata* in "southern Canada" [= Saskatchewan, Manitoba and northwestern Ontario]. The Gopher Snakes and Bullsnake are grouped as *Pituophis catenifer* now separate from the southeastern Pine Snakes (*P. melanoleucus*). Differing from some recent authors, The Western Yellow-bellied Racer *Coluber constrictor mormon*, the Fox Snake *Elaphe vulpina gloydi* and the Northern Pacific Rattlesnake *Crotalus viridis oreganus* are not elevated to species status. The text was apparently completed prior to publication of a revision of the Ratsnake *Elaphe*

obsoleta and the consequent elevation of *E. o. spiloides* to a species (as *Elaphe spiloides*) which now includes all Ontario populations (Burbink et al. 2000; Burbink 2001).

The book concludes with a four-page Glossary presenting an English translation for genus, species, and subspecific names, and an 102-page Bibliography. I did not note any more recent than the year 2000. Citations in the species accounts reference sources for most but the more general statements allowing them to be verified and/or searched for additional information.

Its through synthesis of the literature will make this a standard reference for years to come for both researchers and naturalists with any interest in snakes.

Literature Cited

Burbink, E. T. 2001. Systematics of the eastern rat snake complex (*Elaphe obsoleta*). Herpetological Monographs 15: 1-53.

Burbink, E. T., R. Lawson, and **J. B. Slowinski.** 2000. Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): a critique of the subspecies concept. Evolution 54(6): 2107-2118.

FRANCIS R. COOK

Canadian Museum of Nature, Ottawa, Ontario K1P 6P4 Canada

BOTANY

The Illustrated Encyclopedia of Trees

By David More and John White. 2002. Timber Press, Inc., 133 S.W. Second Avenue, Suite 450, Portland, Oregon 97204-3527, USA www.timberpress.com; hardcover, 800 pages. U.S. $79.95.

This is an absolutely beautiful book. Usually with one and a half pages per species are presented: painted illustrations of trees, flowers, fruits and leaves, often at different stages in spring, summer, fall and winter "found in Britain, France, Germany and the Low Countries – common or rare, native or introduced, growing wild or cultivated in arboreta, parks and gardens", by artist David More.

The accompanying text written by John White describes the native range of each species, approximate time of its introduction into cultivation, where it came from, the preferable habitat, various cultivars and various additional interesting information.

All of this is in family sequence beginning with the Ginkgo family and ending with the Palm family. Over 1000 species are treated.

The book begins with a Table of Contents of two pages, two pages of Foreword and an Introduction of eleven pages with descriptive information including a list of trees for problem sites or special needs. It is completed by a Glossary, an Index of Scientific Names and an Index of Common Names. Its weight is about six pounds and for that reason should be best either kept at home or in an office and not carried into a garden or arboretum.

One thing that was not mentioned in the text is the possibility of a cultivated tree species invading into open or non-cultivated areas. Three species that have spread extensively in some areas in the vicinity of Toronto are Scots Pine (*Pinus sylvestris*), Silver Birch (*Betula pendula*) and Norway Maple *(Acer platanoides*).

WILLIAM J. CODY

Biodiversity, National Program on Environmental Health, Agriculture and Agri-Food Canada, Wm. Saunders Building (49), Central Experimental Farm, Ottawa, Ontario K1A 0C6 Canada

Carnivorous Plants of the United States and Canada: Second Edition

By Donald E. Schnell. 2002. Timber Press, Inc. Portland, Oregon. 468 pages. U.S. $39.95.

This book contains a wealth of information and absolutely beautiful colour pictures of 55 carnivorous plants which occur in the United States and Canada, some as far north as the Northwest Territories, Yukon and Alaska. It is a tremendous step ahead of the author's first edition which was published by John F. Blair in 1976 and numbered 125 pages.

In the new edition, there is a short three-page Preface in which the author calls attention to the changes, developments and explanations in the following text, the elimination of the cultivation chapter, comments about the photographs and thanks to many unnamed individuals and especially to his wife, Brenda.

The next 68 pages are devoted to Carnivorous Plants: An Introduction under the following headings: Carnivorous or Insectivorous, General Characteristics Related to Habitat, Must Carnivorous Plants be Carnivorous? Trapping Mechanisms, How Traps Attract Prey, Carnivorous Plant Communities, Carnivorous Plant Habitats, and Some General Notes on Cultivating Carnivorous Plants. All of these sections contain interesting information.

This is followed by the chapters Venus Flytrap, Eastern North American Pitcher Plants, California Pitcher Plant, Sundews, Butterworts, Bladderworts and Other Possible Carnivorous Seed Plants. Within each of these chapters is easy to read information on the families, genera and species, scientific names, and common names, descriptions, flowering seasons, dis-

tribution, habitats, variations, pollination trapping mechanisms and other interesting information. For anyone with botanical interests this is a most worthwhile contribution.

Biodiversity, National Program on Environmental Health, Agriculture and Agri-Food Canada, Wm. Saunders Building (49), Central Experimental Farm, Ottawa, Ontario K1A 0C6 Canada.

WILLIAM J. CODY

An Eclectic Guide to Trees East of the Rockies

By Glen Blouin. 2001. Boston Mills Press, Erin, Ontario. 280 pages. $29.95.

If you like trees, you must read this book. Actually, if you like trees, you will want to acquire a copy of *An Eclectic Guide to Trees East of the Rockies* for your very own. Abounding with the sort of information identification books don't have room to accommodate, it is an excellent complement to the usual tree field guides.

Glen Blouin loves trees. It's obvious. He writes about them with a tenderness and passion that makes the book hard to put down once you start reading. And he has come to know each tree species so thoroughly (based on considerable experience and research) that he presents details and tidbits you will be hard pressed to find elsewhere between the same covers.

Blouin starts each species profile with an identification page. This section provides the tree's scientific and common name, plus other names in English and French. It also includes the name for the tree in one of North America's many Aboriginal languages. White Birch in Woods Cree, for example, is *waskway*; Hickory in Cayuga, *onenoga*; Red Oak in Pawnee, *nahata-pahat*; Black Ash in Mohawk, *ehsa*; Tamarak in Abenaki, *akemantak*; White Spruce in Ojibway, *zesegaandag*; Chokecherry in Assiniboin, *champah*; Eastern Hemlock in Onondaga, *o-ne-tah*; White Elm in Shawnee, *hani:pi*.

The identification spread also includes a description of the tree's leaf, flower, fruit, twig, bark, wood, height, diameter, and longevity, plus the first of multiple photographs scattered throughout the species profile.

But my favourite part of each profile comes after the identification page. That's where Blouin presents the "eclectic" information which makes this book so extraordinary. For each species, he covers any combination of the following: the tree's history and use by humans, suitability to woodworking and other industrial purposes, traditional uses by Aboriginal North Americans, importance to wildlife and ecosystems, ornamental use and propagation, natural enemies like pests and diseases, conservation issues, and more — the sort of things Blouin calls "relevant digressions." These species profiles reveal each tree as a fascinating character and significant member of a greater community of life.

Here are some facts and figures I found fascinating. The White Elm's leaves are rich in iron, potassium and calcium; and they decompose quickly to improve the soil. Willows apparently interbreed and hybridize freely, making it very difficult to identify individuals with certainty. A fungal disease is seriously threatening the survival of Butternuts in North America; there is fear, in fact, that the butternut might go the way of the American Chestnut. Jack Pine stands on Michigan's lower peninsula are one of the last remaining nesting habitats for the highly endangered Kirtland's Warbler. Small Eastern Hemlocks can exist up to 200 years in the forest understorey, waiting for shorter-lived trees to die and provide conditions for the smaller hemlocks to shoot upwards. Various conifers vie for the distinction of having provided Jacques Cartier with a cure for scurvy. Cottonwoods are the fastest growing native tree east of the Rockies. And Striped Maple leaves provide soft and strong toilet paper in the bush.

That's only a brief sampling of the wonderfully diverse information presented in this eclectic guide to trees east of the Rocky Mountains. My only complaint is that there's no index. Perhaps the publishing budget ran short of money. Perhaps the wide-ranging nature of the content would have made indexing problematic. There's probably a good reason why an index was not included. But I sure miss it, particularly when I'm looking for a particular nugget of information among all those tidbits.

R. SANDER-REGIER

RR5 Shawville, Quebec J0X 2Y0 Canada

ENVIRONMENT

Life, Temperature, and the Earth

By David Schwartzman.1999. Columbia University Press, New York. 241 pages. U.S. $27.50.

There is more to *Life, Temperature, and the Earth* than its title indicates – which is interesting enough in itself. But when I received the book, I was delighted to find that it is also an update and modification of important aspects of the Gaia hypothesis in light of geochemical, geophysical, mathematical, and paleontological data.

The author, David Schwartzman, starts by outlining a theory of biospheric evolution, basically describing the coevolution of climate and life in Chapter 1, "Climatic Evolution: From Homeostatic Gaia to Geophysiology.". He also gives a brief history of the Gaia concept – from Lovelock's early theories to the development of Gaia-related thought through the 1980s and1990s.

In Chapter 2, "The Biogeochemical Cycle of Carbon," Schwartzman explains the carbon cycle, describing it on a geological time scale, and discussing its centrality in contemporary greenhouse debates. In Chapter 3, "Faint Young Sun Paradox and Climate Stabilization," he talks about the standard model of solar luminosity variation over geologic time, the faint young sun paradox, and challenges to the standard model.

Chapters 3 to 5 deal with weathering from a biotic perspective – something naturalists would find particularly interesting. Schwartzman introduces readers to weathering and soil formation, then discusses biotic enhancement of weathering, and the influence of tectonics on climate and weathering. He also looks at field studies and at estimates of biotic enhancement of weathering.

The next two chapters, 7 and 8, are a discussion of Earth's surface temperature. Schwartzman traces Earth's surface temperature history and posits a much warmer Precambrian Earth surface than conventionally believed. He then explores the possible constraints of these warmer temperatures on microbial evolution.

Schwartzman continues with a chapter on the theory of a self-organizing biosphere, followed by implications of all the theories and data discussed to that point on bioastronomy – basically looking at the habitability of terrestrial planets. In the final chapter, he summarizes his main conclusions and suggests future directions for research in fields like climatology, geochemistry, geology, geomorphology, paleontology, biology, biophysics, and biochemistry.

Needless to say, the book is quite scientific, and I must confess I didn't understand all of it. But a reader with perseverence, a keen interest in theories surrounding the concept of a self-organizing biosphere, and a good grasp of the sciences involved, would find this book a worthwhile and fascinating read.

R. SANDER-REGIER

RR5 Shawville, Quebec J0X 2Y0 Canada

City Wilds: Essays and Stories about Urban Nature

Edited by Terrell F. Dixon. 2002. University of Georgia Press, Athens, Georgia, USA. xviii + 311 pages. Cloth U.S. $45; paper U.S. $19.95.

City Wilds is a collection of thirty-five wildly diverse stories, both fiction and non-fiction, about nature in the city and people's experiences with it. It's an intriguing subject because, as Dixon emphasizes in his introduction, we tend to view "wildness" as being far off in wilderness areas.

Yet urban centres are filled with wildness too, as the stories illustrate. And it is increasingly important to raise awareness about urban nature and protect it because, Dixon points out, "The time is past when most city dwellers could draw on knowledge of nature gained during a youth spent in a small village or in the countryside. For the increasing numbers of Americans born in cities, any first-hand, day-to-day knowledge of nature comes from urban nature."

Robert Michael Pyle brings that point home eloquently and directly in his piece "The Extinction of Experience." He talks about growing up with intimate exposure to nature in the city of his childhood: "I grew up in a landscape lavishly scattered with unofficial countryside – vacant lots aplenty, a neglected so-called park where weeds had their way, yesterday's farms, and the endless open ground of the High Line Canal looping off east and west. These were the leftovers of the early suburban leap. They were rich with possibility. I could catch a bug, grab a crawdad, run screaming from a giant garden spider; intimacy abounded."

These childhood experiences helped shape the lepidopterist and nature writer he later became. And, he stresses, that kind of urban nature experience and intimacy is essential to the survival of our planet.

Most of the other pieces don't make this point as directly. But they demonstrate it. From paddling the varied, and sometimes dangerous, waters surrounding New York City, to fly fishing on a downtown creek (a "Zen fishing paradise") that cannot support fish. From planting a flower from childhood memory on an inner city fire escape, to continuing a family farming tradition by cultivating a hidden city vegetable plot. From studying insects, eye to eye, in urban "waste places,"

to letting childhood imagination run wild in an abandoned lot that "could hide things for a thousand years. There beneath the roots of soggy flowers were the bones of murdered pirates and dinosaurs, the eye of a unicorn turned to coal."

It is impossible to do justice to thirty-five stories in one review. So I'll tell you that they're all interesting and personal – some serious or funny, some joyful or sad, some a combination – and that in all their far-flung diversity, each illustrates that all-important intimacy. It's something Lisa Couturier expresses with particular feeling in her "Reversing the Tides" piece about the magic of natural enclaves near resilient urban waterways that "In all their woundedness ... manage to give life."

Here's what she says about her chick monitoring work at a heronry on a delta near New York City: "When our work is finished, we emerge from the heronry carrying an assortment of dog ticks on our bodies and splattered with what we call splooj (our word for the large and liquid bowel movements of baby birds), bird pee, and regurgitant ... But I also carry a gift: an intimacy with the spirits, sounds, and touches of birds. The snowy egret nestlings, so fearful even as I try to calm them, wrap their long reptilian-skinned toes around my fingers in an effort, I guess, to feel safe. The excrutiatingly shy glossy ibises lay limp in my lap while I stroked their dark brown feathers. And although the black-crowned night herons assertively nip at me, I admire their aggressiveness; it helps them survive. The colours, habits, feathers, pecks, personalities, smells, movements, eyes, and cries of these birds are inside of me. I, quite simply, love them."

It is a love and an intimacy naturalists can easily identify with. And *City Wilds* is a story collection book-loving naturalists would appreciate. I myself read the book too quickly the first time around. I would like to go back and re-read many of the stories, one at a time, with space in between to savour each one ... intimately.

R. SANDER-REGIER

RR5 Shawville, Quebec J0X 2Y0 Canada

Conservation Biology

By Andrew S. Pullin. 2002. Cambridge University Press, Cambridge, United Kingdom; New York, USA. 345 pages. Cloth U.S. $120; paper U.S. $45.

The discipline of conservation biology has taken a prominent position among the sciences. As demand for highly trained practitioners of conservation biology increases, so does the number of general text books available for use by educators. *Conservation Biology* by Andrew Pullin is a newcomer to the list of possible texts vying for position as THE ultimate learning resource. This specific book was intended to serve as an undergraduate text or supplementary reader and assumes a background in basic ecology. Pullin incorporated three significant changes that alter the cosmetics and content substantially over other undergraduate level texts. First, his book focuses more on the United Kingdom and Europe than on North America as seen in other leading texts. Second, unlike the other competing texts in the field of conservation biology, he has excluded material that does not fall within the realms of natural science such as policy, economics, and other human dimensions. Third, he has included information that has not been well covered in other treatments such as the conservation of "processes". Each of these changes is worth further discussion as these are really what differentiate this text from the others.

The decision to expand the geographical focus of the text beyond primarily North American focus is admirable. This expansion in focus would have been particularly evident had Pullin incorporated more human dimension sections that discuss policy and legislation that is typically based exclusively on issues from the United States (e.g., US Endangered Species Act). In the end, the text is clearly regional, emphasizing the United Kingdom and the rest of Europe. As such, this text would be particularly relevant to undergraduate courses in those locales. Pullin does provide some excellent examples from the rest of the world, but I believe that room still exists for a "non-regional" and balanced treatment that is globally applicable. Unfortunately, this text does not fill that void.

Pullin has omitted much of the material on human dimensions due to what is described as a traditional poor treatment in other conservation biology texts. I agree that few if any of the existing conservation biology texts are sufficient on their own at presenting social science and economic issues, but they do serve as starting points. By excluding human dimensions from the table of contents, it only helps to polarize the natural sciences from the social sciences. Indeed, one of the themes that makes conservation biology unique is its interdisciplinary nature and this point should be emphasized, particularly in an undergraduate text.

The text is also arranged in a manner that differs from convention. Foremost, I want to state my excitement about the chapters on landscape ecology (12) and the conservation of evolutionary processes (13). These chapters are rather unique to conservation biology texts and are well deserving of inclusion. These chapters are well written, interesting, and worthy of dissemination to students. However, there are several earlier chapters for which the same can not be said. The first section on biodiversity and global ecosystems (Chapters 1 and 2) is extremely simplistic and is not appropriate for this text. The author prefaces

this section by suggesting that many students may wish to skip this section. I agree and wonder why this section was not strengthened to make it compatible with an undergraduate level course. The theme of oversimplification is evident in other parts of the text as well. The chapter on biotic effects (4) is very broad, but lacks depth on important concepts, particularly those dealing with conservation genetics.

In conclusion, this book does have several qualities that separate this contribution from the existing suite of texts and make it a worthy addition to the series of complementary materials used in developing an undergraduate course. However, the book lacks sufficient background in ecology and evolutionary concepts to serve as a stand alone text. In all fairness, the author acknowledges that the book is best supplemented with material and to that end the author provides numerous information sources (including web sites and literature). Furthermore, I found the order of materials and general organization clumsy. The simplistic nature of many of the chapters will limit the use of the text in graduate training. The writing is clear throughout, but the depth of treatment is inconsistent among and within chapters. The book is well illustrated using colour plates and has ample examples from the primary literature that encompass a variety of taxa. The publisher's arrangement of material on the page does result in significant "white space" that could have been used for fleshing out topics that were inadequately covered. This book adds to the suite of texts available to educators. However, I feel that this text is in similar company with Hunter (2001), and not nearly as in-depth or complete as Meffe and Carroll (1997) or Primack (2002). Beyond academic circles, I doubt this book will have much appeal to groups such as naturalists. As this book is written as a course text, the nonacademic reader will find the writing style and content unfulfilling.

STEVEN J. COOKE

Centre for Applied Conservation Research, Department of Forest Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4 Canada

Ecological Basis for Stand Management: A Summary and Synthesis of Ecological Responses to Wildfire and Harvesting in Boreal Forests

Edited by S. J. Song. 2002. Alberta Research Council Inc., Vegreville, Alberta, Canada. 329 pages.

It appears that this book is supposed to be an attempt to reverse the notion of that "Albertans who have seen logging practices tend to have a more negative view of the forest industry". This publication is a true mirror of the current state of art of natural resources. Mis-managed fisheries resources lead the way, very closely followed by forestry and other resources. "Harvest rates have risen 4 fold over the last 32 years in Alberta ...", and despite all the glossy statements about sustainability, it's not a secret for any informed conservationist that the global timber demand cannot be sustained any further, and certainly not in Western Canada (as constantly reduced harvest rotation periods show, for instance).

This book is nicely structured into 13 Chapters and has 27 Tables, 30 Figures and 5 Appendices. Each chapter offers a descriptive Text, Highlighted Text Sections, Emphasized Key Findings, Summary Table, Condensed Management Implementations, Future Research Needs and References. Although the book chapters are supposed to provide guidance for forest managers and practitioners, I would say due to the lengthy text (329 pages) managers will not read it, nor would I really recommend them doing so. If this book is supposed to be used as a sole resource to manage Forest Stands in Alberta, I would be really worried. For instance, the biodiversity issue, or rare vascular plants, are not addressed at all; instead White-tailed Deer issues are well covered. Already the book title leaves it undefined "which" boreal forest is meant: the one in Scandinavia, Russia, Alaska or Canada? I am sure this book is not a global guide how to manage boreal forests world-wide since no Russian references are quoted (but Minnesota's Forest is cited several times). Unfortunately, this is not simply a book by 13 Forest Consultants funded by the Albertan Forest Industry and Government Complex; university-based researchers are involved. Thus, this book seems to represents the current (conservation) state of knowledge on boreal forestry for a large part of North America (a huge and globally important forested land mass). Considering its global importance, the weak guidance provided and the lack of hard facts presented in this book appears pitiful, if not scary.

The overall scheme pursued in this provincial publication is already ambiguous enough: does fire equal harvesting ? The answer for this question is, in most chapters: yes, almost. Other paradigms which the authors try to hammer home to the readers are that Residual Tree Retention would usually be good, forest harvest could mimic fires, convergence after 60 years to natural forests would occur, and forest edges older than 25 years hold no edge effect anymore. The authors seem to think that the boreal forest is a relatively simple ecosystem with few players, and thus this book deals mostly just with Aspen and Spruce.

For my taste, this is a big book reporting on imprecise and lacking information. A bigger book does not make automatically for a better book. The reader will not learn about the reasoning why a Riparian buffer zone of 200 m is used in Alberta. The concept of presenting statistical confidence intervals, rather than averages and qualitative information, appears to be foreign

to the producers of this book. Truly quantitative and precise text sections are basically unavailable for most parts, and the extensive use of "could", "may", "perhaps" and "potentially" severely waters down the message to managers. "Persistence of birds" is another one of such soft terms, adding confusion and making sound decisions and even constructive discussions on forest and conservation management difficult. Whoever can define and evaluate such politically loaded terms as "risk" or "...protecting native ecosystem integrity..."? So many investigations of this book deal with resource use vs. availability, but a sound Resource Selection Function implementation is missing throughout the entire book. The book does not present any maps whatsoever, and thus, spatial ecology considerations (an entire ecological dimension) are missing, too. Even basic topics like site index and elevation gradients are not elaborated on. Although the book is centered on forest "stands", ecologically there is no such a thing like a "stand" and it's hard to agree on what constitutes one.

Ornithologists will find the Chapter on Birds (usually a key species group of global interest to naturalists and conservations) weak, e.g. when it comes to bird abundances and communities; although, the forest edge section is generally an interesting read. It's incredible indeed that the bird chapter does not mention neotropcial wintering grounds as being important for birds in the boreal forest. The issue of bird densities (absolute densities) comes up several times, but I feel that most of the mentioned bird surveys just deal with a relative index of abundance instead (an entirely different concept, and statistically less powerful). I found the management statements relating to birds really confusing. Simply reading the extensively cited publications by Hobson and Schieck (1999) and Schieck and Hobson (2000) will provide most of the information for this chapter. The assumption that bird abundance would equal nesting success is not further addressed. A potential strategy to manage bird communities is outlined, but the authors themselves call it "best guess" which still would need to be tested in an adaptive management framework. I am unclear why such things should be helpful to forest managers unless one wants to build forest management on best guesses, rather than sound science. The views of First Nations are not presented.

On the good side, the summary of the Mammal Chapter is quite readable, and the summarizing tables at the end of most chapters can be informative for managers. The choice to include a Chapter dealing with 22 non-vascular species such as moss and lichen is fantastic indeed! So is the chapter on the effects of wildfire on forest soil properties. This publication is also great in summarizing literature of various topics on boreal forests covered in the 13 Chapters. Besides the many Canadian and international peer-reviewed publications cited, this book must present the ultimate pool of not-peer-reviewed grey literature publications for the boreal forest.

Sometimes when reading the text, one is not sure whether to laugh or to cry about statements made in the book such as "Less common species often disappear", "Residual patches incorporate old-growth structure into cutblocks", "Many plants survive harvesting", or "As patch size increased, bird communities became less dominated by open country species and more dominated by forest species". Rightly so, the book states "An area proposed to be harvested cannot be 'sacrificed' with the justification that other suitable habitat remains in the landscape".

The book indicates that the occurrences of exotic species in boreal forests are linked to human activities and traffic. The ambiguity that forests are managed based on the natural disturbance paradigm mimicking burned conditions in cutblocks are very obvious, e.g. when it comes to mammalian abundance and diversity. As this book shows, even basic information on bats in the boreal forest is missing, and can only be speculated upon (thus, a sound and sustainable forestry recognizing bats is basically impossible).

Another Canadian forestry classic is the presented strategy and so often referred to as "Coarse Filter Approach". My concern comes in that this is simply a nice sounding excuse for poor and low-cost data and research, but then in the political forum it can suddenly be interpreted in detail and however managers and politicians see fit.

Among conservation circles it is highly debated whether first rotation forests really return to a virgin state (as stated by the authors). I am still puzzled whether Forest Fires are complementary or additive to the ongoing forest harvest, rather than just complementary (as suggested in this book).

The decision not to address the ecological implications of a vast range and combination of silviculture techniques is unfortunate and reduces the relevance of this report. At least, the importance of nitrogen is described as a major factor affecting forest productivity. Three major stages of forest success are elaborated on. Interesting statements are provided on what shaped the public attitude towards forest edges.

This publication is likely meant to be an Alberta forestry flagship publication and thus its support by Alberta Research Council, Alberta-Pacific Forest Industries Inc., Manning Diversified Forest Products Ltd., Alberta Sustainable Resource Development, Ainsworth and Northern Rivers Ecosystem Initiative. However, considering that many Forest Companies in Canada are owned and directly influenced by foreign countries (e.g. U.S., Japan, Norway and also European Markets), the reader is advised to inquire what is to be found behind such company terms, e.g. in regards to international ownership, governmental efforts and subsidies. In the introduction to the book, the authors even admit that the topics presented are limited by concerns of funding partners!? Such a funding scheme and its implications are classic concerns and ones which are so heavily criticized in the public nowa-

days: the political complex of federal and provincial governments, global industry and industry-close NGOs drives the agenda. On a global scale, and as this book shows, the citizen is more and more delivered to the corporate world, without any relevant input. The request made in this book that the public needs to be involved in public land decision-making is already clearly contradicted by the fact that none of its relevant research; or GIS-data are freely available; e.g., as a database for download on the WWW.

Overall, this book is a great reflection on what provincial governments and industry in Alberta can achieve, and what they can not. Smaller typos and wrong references may be forgiven. One may ask the question: who may benefit from this book, who buys it? The original price of over 100 CAN$ for this book was fortunately soon dropped towards a free PDF download. However, as the authors state, "The clearcut generally presents a strong negative image, that is not only perceived as 'ugly' but has also come to symbolize a host of negative traits including a lack of respect for nature, destruction of biodiversity, and ecological integrity, corporate control, and lack of public participation in land use decisions". This book fails to change this situation.

FALK HUETTMANN

Geography Department, University of Calgary, Calgary, Alberta T2N 1N4 Canada
Present address: Biology and Wildlife Department, University of Alaska, Fairbanks, Alaska 99775-7000 USA.

Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests

By Lee E. Frelich. 2002. Cambridge University Press, Cambridge, UK. 266 pages.

Disturbance is ubiquitous in forest ecosystems. Forested landscapes are best viewed as an integration of climatic, biotic, edaphic and geomorphic processes that determine the character of disturbance events occurring over a wide range of temporal and spatial scales. Disturbed by the extremes of either catastrophic, stand-replacing events that may include fire, insect outbreaks, and extensive windthrow, or periodic, small-scale gap processes mediated by fungal pathogens, forests are in constant flux when viewed from a landscape perspective. Such a wide range in the periodicity, intensity and scale of disturbance events, and the diversity of bio-edaphic interactions creates a complex, fluid, heterogeneous landscape.

Lee Frelich, founder and director of the University of Minnesota Center for Hardwood Ecology, introduces the reader to the significant disturbances that have shaped, and continue to shape, the hemlock-hardwood forests of the northern regions of the Lake States (Minnesota, Wisconsin, and Michigan). For the past two decades Dr. Frelich has dedicated himself to understanding the stand- and forest-level dynamics of these deciduous-to-boreal transition forests. He forms part of a long tradition of university and government (United States Forest Service) forest ecology research, much of which is scattered in scientific journals and government reports. *Forest Dynamics and Disturbance Regimes* provides for the first time, in an engaging, well-illustrated, and synthetic format, the fruit of this rich research legacy.

"Under what conditions do forests change or stay the same?" Thus might one summarize the intent of this book. Introductory chapters set the scene by describing the Great Lakes temperate forests and their disturbance regimes dominated by fire, wind, insect outbreaks and mammalian herbivory. Of significance to the practicing forest ecologist will be the chapter on sampling and interpretative techniques used to detect and interpret forest disturbance regimes. Emphasis is placed on the use of tree radial increment patterns as a valuable source of insight into stand disturbance history.

Frelich emphasizes the critical role played by disturbance in both stand development and forest succession. He properly distinguishes between stand development and succession, both of which are often confused in the literature. Disturbance will always initiate a new cycle of stand development in the regenerating, post-disturbance forest. However, disturbance may or may not initiate a species change or a new successional sequence.

Consideration is also given to the differing effects of disturbance on both the stand- and landscape-level. This distinction is important, especially given the wide temporal and spatial scales at which disturbances may occur. Furthermore, instability on the stand level may be interpreted as stability on the landscape level. Interpretation often depends on the scale of investigation.

A particular strength of this work is Frelich's ability to engage the complex interaction of different disturbances. Frelich not only introduces the wide diversity of temporal and spatial patterns of forest change, but even more importantly, highlights often counter-intuitive insights into forest change and continuity. I found the following particularly noteworthy: (1) the nonlinear response of forest species composition to disturbance severity, (2) the cause and development of patchy hardwood-softwood mosaics, (3) clarifying taxonomy of the concept of old-growth, (4) how different forest types can exist on relatively homogeneous sites, and (5) the multiple successional pathways open to any particular forest type. Frelich's final chapter summarizes the notion of forest stability. It provides conceptual mod-

els of forest response to disturbance, 3-D models of succession in different forest types, and a final classification of four different types of forest landscape.

This work is particularly important as humans continue to "disturb" forests, especially by commercial forestry. Before any claims can be made about the desirability of the changes created by human interventions, it is essential to properly comprehend the range of natural forest disturbance regimes and the associated changes in forest structure and tree species composition.

The book addressees the scientific community and would properly be of greatest interest to forest ecologists and to all students of forest change. The judicious mix of empirical case studies, hypothetical examples and conceptual models helps the reader to think "beyond the box." The many line drawings, flow charts and black-and-white photographs help to clarify the different concepts.

As one is reminded in the subtitle, this book focuses exclusively on the temperate evergreen-deciduous forests of the Lake States. While it is certain that many of the concepts developed from research in this forest type are applicable to other forest types, it is wise to resist any quick and easy transfer of ideas. Forests grow in conditions that span a wide ecological spectrum, a situation that often resists our human tendency to categorize and classify. Be that as it may, this book provides rich and substantive insight into this well-studied and much loved forest region at the deciduous-boreal interface.

JOHN MCCARTHY

St. Mark's College, University of British Columbia, 5935 Iona Drive, Vancouver, British Columbia V6T 1J7 Canada

The Sacred Balance: A Visual Celebration of Our Place in Nature

By David Suzuki and Amanda McConnell. Greystone Books, Vancouver, British Columbia, 151 pages. CDN $55.

With over 100 pages of illustrations and its large page format, this book may at first glance appear to fit into the "coffee table" book genre. However, a closer read reveals a somewhat more substantial literary content. This book is an interesting juxtaposition of science and art that explores the role of humans in the earth's global ecology. The authors describe aspects of human ecology in ways that make the ideas accessible to the non-scientist, weaving story-telling, poetry, and creative analogies into the text. The book makes lavish use of illustrations to demonstrate ways in which humans are inextricably linked to our global ecosystem. The eclectic collection of photographs portrays life ranging from views of bacteria under a microscope to satellite panoramas of the earth. The images capture some stunning landscapes and unique views of human personality and culture, making this book a worthwhile purchase for its photographic merit alone.

Suzuki and McConnell begin by introducing the view widely held in many aboriginal cultures that the environment is not something separate from humans but rather that we are part of the earth. Viewing humans as part of the ecological community is not a new idea. It was the view espoused by Aldo Leopold and others more than a century ago, and the concept that epitomized the roots of the conservation movement. However, Suzuki and McConnell add a fresh perspective to this paradigm. The authors classify seven elements that connect humans with the earth: water, air, fire, earth, biodiversity, love and spirit. Each of these themes, plus the introduction, forms the basis for the book's organization into eight chapters.

The first section of the introduction skips hastily from big bang theory and the origins of multi-cellular life to biodiversity, global ecology, and human cultural evolution. The rapidity with which complex scientific concepts are very superficially reviewed in the introduction is at times cumbersome. Covering so much ground in a short span of text leaves the reader feeling somewhat like they've covered the history of planet earth in fast-forward. Nevertheless, the authors do make successful albeit brief explanations of many complex concepts through their use of creative analogies. For example, in explaining the uncertainty of the effects of genetically modified organisms, the authors explain,

> "This situation is comparable to pulling Bono out of U2, popping him into the middle of the New York Philharmonic Orchestra, and asking him to 'do his thing' with them. Sounds will emerge, but we certainly cannot anticipate the musical nature of the output."

Such quirky references to popular culture and common human experiences are used creatively throughout the chapters of this book. The second section of the introduction draws on experiences from David Suzuki's professional and private life, and presents an enlightening personal view of our place in nature.

After rushing through a myriad of concepts in the introduction, the proceeding chapters present information in smaller, more digestible chunks, with succinct and thought-provoking chapters exploring each of the seven elements. The authors draw expertise from fields as diverse as biochemistry, toxicology, psychiatry, cosmology, ecology, and anthropology. Each chapter concludes with a series of photographs, poetry, and quotations that further illustrates the chapter theme. Given the somewhat dense introductory chapter, I was surprised to find no concluding chapter providing some interpretation and synopsis of the mix of ideas. This was perhaps deliberate on the part of the authors, leaving it up to the reader to draw their own conclusions. Nevertheless, the concepts of the book are per-

haps best summarized by the concluding words of the introduction, which leave us with the statement that "If we can grasp that we *are* the world we depend on, then we will find where we truly belong and get on with seeking a way to live in harmony within a rich, vibrant community of living things."

This book is a unique and insightful pictorial exploration of the complex relationships between humans and planet earth. The book is both aesthetically attractive and intellectually engaging, making it an excellent gift for either scientist or layperson with an interest in natural history and conservation.

LESLEY EVANS OGDEN

UBC Centre for Applied Conservation Research, Forest Sciences Centre, 3rd Floor, 2424 Main Mall Vancouver, British Columbia, V6T 1Z4 Canada

Great Wildlife of the Great Plains

By Paul A. Johnsgard. 2003. University Press of Kansas, Lawrence, Kansas, USA. 309 pages.

Great Wildlife of the Great Plains is a narrative book about the species representative of the Great Plains, from the grasslands of Texas to the mixed prairies of Canada. The text highlights 121 species of birds and mammals, with each chapter covering a different geographic area. After a short introduction describing the different geographical regions, Johnsgard presents eight chapters based on geography: (tallgrass prairie (Chapter 2), mixed-grass prairie (Chapter 3), shortgrass prairie (Chapter 4), sandhills grasslands (Chapter 5), arid shrubsteppes (Chapter 6), riverine and upland hardwood forests (Chapter 7), coniferous forests and woodlands (Chapter 8), and prairie wetlands (Chapter 9). The last three chapters take a different approach, with an overall presentation of the most common wildlife species (Chapter 10), then seasonal or occasional species (Chapter 11 "Migrants and drifters"), and concludes with a chapter discussing some of the recurring themes and conservation challenges (Chapter 12 "What is still so great about the Great Plains"). This last one invites the reader to visit this region, even if only "Armed with an inquiring mind and a field guide or two..." (page 212).

The book has a well-recognized bird bias: the author readily admits the bias in the preface (page xiii), and warns that the coverage is 61% birds, 23% mammals, and 16% reptiles and amphibians (based on 121 species discussed). However, my perception is that the book emphasizes birds even more, and I would have to guess that 75% of the actual text refers to birds, a bias likely arising from the author's expertise and background being mostly ornithological. The bias is less pronounced in the illustrations, with 73 figures devoted to birds (50%), mammals (33%), reptiles and amphibians (10%), and geographic maps (7%). The book does present most species of interest, but maybe one interesting species missing is the raccoon (see species index pages 305-309). Although the latter is not an "icon" of the Great Plains, this species is of great interest since it has been colonizing the northern prairies recently.

The format is pleasing, and the drawings help illustrate the species mentioned. Perhaps even more useful is the provision of five appendices illustrating tracks and sign of Great Plains species (Appendix 1), a list of nature preserves and natural areas (Appendix 2), a list of birds (Appendix 3), a list of mammals (Appendix 4), and a list of reptiles and amphibians (Appendix 5). The lists are not exhaustive, and do contain some errors in scientific names (see black-footed ferret, page 258, and nutria page 262). Nonetheless, they provide the reader unfamiliar with the Great Plains a good idea of which species can be found in which habitat and what states.

The book is narrative, and the prose makes it more palatable for lay audiences. The author's anecdotes of his childhood in North Dakota are often referred to (examples on pages 17, 19) and, in my opinion, add a "real-life touch" to an otherwise informational piece. The book is probably most valuable as an overview of what species are found in each geographic region, and in that respect, is best suited to those unfamiliar with the respective areas. To the latter, this book leaves few stones unturned, and is a good addition to the naturalist interested in learning more about the Great Plains and the wildlife to be encountered therein.

SERGE LARIVIÈRE

Delta Waterfowl Foundation, R.R. #1, Box 1, Site 1, Portage la Prairie, Manitoba R1N 3A1 Canada

Present address: Fédération des Trappeurs Gestionnaires du Québec, 1737, rue Champigny Est, Sainte-Foy, Québec G2G 1A6 Canada

The Last Island: A Naturalist's Sojourn on Triangle Island

By Alison Watt. 2002. Harbour Publishing, Madeira Park, British Columbia. 192 pages. $34.95.

Most of this book (pages 15-157) consists of a chronicle of a single field season (late April to 1 September 1980) spent by the author as a field assistant to the late Anne Vallée on the western-most of the Scott Islands off the northwestern tip of Vancouver Island. Triangle Island is famous as the site of an exceptionally unsuccessful lighthouse (too often shrouded in fog) and for its colonies of seabirds. One of these seabird species, the Tufted Puffin, was the subject of Vallée's study. Watt's chronicle is written in diary form and is partly a diary, but is also embellished with details of various aspects of the flora and fauna of the island gleaned from the literature and from conversations with other biologists, as well as historical events and native beliefs along British Columbia's west coast, personal reminiscences, dreams and random thoughts by the author. An introduction (pages 9-13) and "part two" (pages 158-174) chronicle another brief sojourn in August 1996. Watt's text is supplemented with several illustrations of plants, sea life and birds, mostly in colour, with a series of "notes" (pages 179-183) expanding on various biological, geographical and historical details and by a "selected bibliography," guiding the interested reader to sources for more detail on the island, the biology and natural history of some of the species mentioned, the culture of the tribes who frequented the area before Europeans arrived and other topics mentioned in the text.

The book presents a wide sweep of the fauna, flora and geology of Triangle Island and its offshore waters, but it does not offer complete coverage of its natural history. Rather, it presents a sample of the author's observations, sometimes in the context of other local or world-wide knowledge. Apart from a few brief comments and some of the drawings, it offers little in the way of "field guide" elements, as claimed on the dust jacket, but is best described by that dust jacket's characterization as "an intimate memoir." Since I spent a month on the island, I found much of interest in its numerous natural history snippets. For those who haven't been there, its appeal will also lie primarily in these snippets. The author's skill at presenting the joys and tensions of spending a prolonged field session in close quarters with one other person on an isolated island rich in natural history under highly variable, often rapidly changing weather conditions also provides insight into the sociology of scientific field research.

Watt's research appears to be reasonably thorough and I found few outright errors in the book. Birds are not actually born (pages 74 and 163) – they are hatched. Two genera are not italicized (*Laminaria* on page 96 and *Noctiluca* on page 101), and a few minor grammatical errors escaped editing. As most countries now use metric measurements, the English dimensions of the island (pages 93 and 95) should have been translated into metric for the sake of younger Canadian and other non-U.S. readers. As suggested by its title, the selected bibliography is far from complete, but lists enough references on the island's natural history to guide the reader to more detail. Before reading the book, I checked the index for Green-winged Teal to see whether or not the author had seen some feeding behaviour that interested me during my stay there. This species was not included in the index, but is mentioned briefly on page 144. Curious as to whether or not this was a singular omission, I checked the index for six other species mentioned in the same paragraph (pages 144-145) and found none listed, suggesting that the index is as selective as the bibliography.

In short, Alison Watt's words, paintings and drawings provide colourful examples of several floral and faunal elements of Triangle Island, as well as interactions among some of these elements, information on how some of the knowledge gleaned there fits into the "bigger picture," and the effects that living in near isolation have on the thoughts of field researchers. It provides an interesting introduction to the island's rich natural history, but is not a comprehensive treatise on it.

MARTIN K. MCNICHOLL

4735 Canada Way, Burnaby, British Columbia V5G 1L3 Canada

Nature by Design

By Eric Higgs. 2003. MIT Press, Cambridge, Massachusetts and London, England. 0-262-58226-0. 341 pages. Cloth U.S. $68; paper U.S. $27.95.

Nature by Design is a noteworthy exploration of the philosophy of restoration ecology. Beginning with a compelling look at the issues and complexities surrounding the management of Jasper National Park, Eric Higgs walks the reader along a path that explains what ecological restoration is, how and why it is practiced, and the many philosophical issues that weave through the concept(s) of restoration. The core of this book centers on the changing meanings of restoration and nature while the act of restoration itself, becomes increasingly technological.

Written for both the novice and experienced in the field of restoration ecology, Higgs' book is imaginatively organized. In the first chapter, Higgs does a first-rate job of highlighting the philosophical problems of restoration, with a poignant example comparing Jasper National Park and Disney World's themed Hotel,

the Wilderness Lodge. I found Higgs' thoughts on the concepts of wilderness vs. wildness and "freak landscapes" enormously interesting. In the second chapter, the reader is introduced to three diverse restoration projects from around the world. These projects differ in their scale, intent (or goal), and method and serve well the ideas posed in the remaining chapters – Higgs regularly comes back to these examples to illustrate a point. Chapter 3 explains what ecological restoration is and provides some history to the restoration movement. It is unusual that the subject of the book isn't properly defined until the middle, but Higgs makes it work and the book flows like a good story.

The concept of historicity is central to the fourth chapter which asks the restoration ecologist how the reference condition (or the state to restore a place back in time to) is decided. It is this chapter where the course of the book changes and the reader starts on a more philosophical journey. Chapter 5 explores the issue of commodification and the increasing technological nature of restoration while Chapter 6 explores the alternative, a more traditional approach founded on community based initiatives. In the final summary chapter, the author effectively brings all his examples and arguments together and suggests that in order for ecological restoration to prosper into the future, we must communicate effectively with each other and not sit idle as landscapes all around us rapidly grow outside the historical range of natural variability.

Following the text of the book, rich footnotes give the reader both valuable reference and provocative anecdotal information. More information is contained in the bibliography which is followed by an ample index.

Higgs's writing style is clear and fluid. The narrative, filled with personal accounts and stories, is not something to be read quickly. It takes time for the concepts and ideas to sink in and take shape to hold a deeper meaning. Those looking for specific instructions on how to accomplish a restoration project will be disappointed. However, this book would be required reading for anyone in the field of ecological restoration, and more than just an interesting read for the general reader. Further, the casual reader may get just as much out of the book by reading only the beginning and concluding chapters which concisely sum up the thoughts and arguments, instead of plowing through the entire text. This is a testament to the author's skill.

Higgs openly states that this book is for an audience who are looking for ways to solve problems – environmental in nature – in a better way. However, like any good philosophy book, *Nature by Design* asks more questions than it answers.

KIRK MONTGOMERY

Department of Geography, University of Calgary, Earth Systems Modelling Lab, Earth Sciences Building, Rm 356, 2500 University Drive N.W. Calgary, Alberta T2N 1N4 Canada

Present address: 410-8604 Gateway Boulevard, Edmonton, Alberta T6E 4B6 Canada

Spreadsheet Exercises in Ecology and Evolution

By Therese M. Donovan and Charles W. Welden. Sinauer Associates Inc. Sunderland, British Columbia. 556 pages. $38.95.

Spreadsheet Exercises in Conservation Biology and Landscape Ecology

By Therese M. Donovan and Charles W. Welden. Sinauer Associates Inc., Sunderland, British Columbia. 464 pages $41.50.

A core component of biological study is the suite of theoretical models that researchers have developed to describe and forecast biological phenomena. Browse through any introductory ecology textbook and you'll find models for nearly every quantifiable biological process. Models are used to answer questions in every area of natural history study: what is a sustainable harvest level for a fishery? what is the likelihood that a rare species will go extinct? what is the best foraging strategy for a particular animal? With their *Spreadsheet Exercises*, Donovan and Welden present a series of computer-based assignments to guide students through the development and application of models to a variety of such ecological and evolutionary scenarios.

The intended audience for these books is undergraduate biology students for whom each chapter provides a practical exercise to complement course lectures. The first six chapters of each book provide a brief review of basic statistics while introducing the concept of computer modelling. As the target audience likely has or will receive instruction in biological statistics the treatment here is very light – just enough to refresh the fundamentals and introduce the novice to key concepts.

The remainder of each book is given over to the exercises. Each chapter begins with a brief theoretical review followed by step by step instructions explaining how to convert the theory into a computer simulation. Some of the chapters stand alone, but generally the later chapters within a section build upon earlier work. For example, in the ecology section the chapter on reproductive value assumes previous completion

of exercises on life tables, geometric and age-structured population models, and survivorship curves. The progression is well thought out: the experience I gained from working through the simpler models and theories of earlier chapters was good preparation for the complexities of stage-structured matrix population models encountered in Chapter 14. Having spent a fair bit of time struggling with these algebra-heavy models in the past, I was pleased to find that several key concepts became clear when I had completed the chapter.

From the beginning the authors adopt an exploratory approach, guiding the reader through the use of spreadsheets to illustrate mathematical concepts. Using spreadsheets allows for easy experimentation, instantly revealing the consequences of altering formulas or model parameters, and encourages independent exploration of the models. Models are by definition abstractions, and I found the exercises very effective in translating the sometimes esoteric mathematical concepts into concrete numbers and informative graphs. Each chapter required between one and two hours to work through, a reasonable evening's diversion for the aspiring ecologist.

Some exercises are more successful than others. Generally, I thought the ecology section was very well done. The population and demography models lend themselves to this sort of presentation, and the authors do a good job of organising them in an engaging way. The evolution chapters were less consistent. Some of the basic concepts, such as Hardy-Weinberg Equilibrium, were clearly laid out. However, I don't think the model used to illustrate gene-flow and population structure was as effective as it could have been. The section on landscape ecology is generally weak. The ideas they try to present here are too complex to allow for easy partitioning into manageable chapters. There were also a handful of typos or minor errors which made some examples unintentionally difficult.

To properly take advantage of the exercises readers will need access to a computer with a recent spreadsheet program installed. The authors have chosen to use Microsoft Excel 98 for their examples. As this is one of the most widely used programs this is a reasonable choice. Many of the exercises use features not available in earlier versions of this program, and people using spreadsheets from different companies may have to spend some time figuring out how to convert the Excel-based instructions to suit their program.

While the *Spreadsheet Exercises* are published in two volumes, this is not intended as a set. More than half of the chapters are shared by both books. Both books have the six introductory chapters. The *Ecology and Evolution* edition is then divided into an ecology section: population, demographic, niche, and succession models; and an evolution section: genetic, selection, and mating system models. The *Conservation Biology and Landscape Ecology* edition contains many of the same chapters under the heading conservation biology, and seven chapters on aspects of landscape ecology: edge effects, reserve design, and landscape statistics. It's unfortunate that the chapters on population viability analysis and harvest models appear only in the *Conservation Biology and Landscape Ecology* edition. These would have been a strong addition to the *Ecology and Evolution* edition. The landscape ecology section requires further development and perhaps an entire book of its own. As is, it left me feeling it was an unfinished last minute add-in.

All things considered, I think the *Ecology and Evolution* edition will be a valuable addition to any undergraduate course in either discipline – indeed, it has already been adopted in biology courses at several universities. The question remains, will it be of interest to naturalists generally? If your interest in natural history is strictly field-oriented, as a botanist, birder etc., probably not. But if you have an interest in biological theory, enjoy math puzzles and learning new tricks on your computer, I think you'll find this an engaging way to introduce yourself to ecological concepts. *Spreadsheet Exercises* isn't the sort of book that will find a place of honour on your reference shelf, but it might help you to better understand the books that have.

TYLER SMITH
5900, rue Monkland, Apartment 10, Montreal, Quebec H4A 1G1 Canada

Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis

W. F. Morris and D. F. Doak. 2002. Sinauer Associates Inc., Sunderland MA USA. ISBN 0-87893-546-0 paperback US $41.95.

This is a great book which should affect how we research and manage wildlife and its controlling factors. The topic of a Population Viability Analysis (PVA) is not really new, but there are only a few books that describe the topic well for the general public and managers. "PVA is the use of quantitative methods to predict the likely future status of a population or collection of populations of conservation concern".

"The promise that PVA holds as a tool for guiding conservation decision-making has been recognized by governmental science advisory boards, by professional organizations such as the Ecological Society of America and by nongovernmental conservation organizations such as The Nature Conservancy." This statement also holds for the Habitat Conservation Plans and for the Recovery Plans of the U.S. Endangered Species Act. However, "Instead of seeing PVA as a valuable tool to aid their decision making, most field-oriented conservation biologists retain the misinterpretation that PVA models can only be constructed and understood by an elite priesthood of mathematical population ecologists".

Fortunately, this book is supposed to make PVAs easier to understand. It is based on the advanced

matrix-based population modeling concept and uses count-based and demographic PVAs. The authors actually present a very good introduction to demographical population studies and even to the relatively new AIC concept. It explains its concepts with examples from a great variety of different animal and plant populations world-wide. The authors make a great effort to explain important concepts such as Vital Rates, Lambda, Bonanzas and Catastrophes, Density Dependence, Ricker Curve, Beverton-Holt Model, Log-Population Growth Rate, Accounting for Errors, Environmental Stochasticity, Sensitivity Analysis and many others. As a key take-home message from this book I see the authors' focus on confidence intervals, rather than the pure population means. Such an approach embraces the uncertainty among population estimates in a much more transparent fashion than is usually done. Many conservationists world-wide have encountered the sad but so often true statement made by the authors: "While data uncertainties are frequently used as a reason to rely solely on expert opinion – or on simple political expediency – when deciding difficult issues, we believe that use of more formal analyses can frequently benefit conservation practice. In the absence of such scientific analysis of conservation situations, personalities, politics, and dollars will drive what actions are and are not taken, often with little or no regard to their real conservation value".

The reader will also learn in this excellent PVA-book about the great importance of the extinction-time cumulative distribution function, plotted against years into the future. As the authors show, there are five measures to express extinction risk: the probability of extinction by a given time, the probability of extinction ever occurring, and the mean, median and model times to extinction. Of these, only the first three are the most useful, but the last two are still the ones most often used.

This book has contributing software in MATLAB and SAS code (also available on the website www.sinauer.com/PVA/), which the practitioner will benefit from. Fourteen pages of literature references and a well organized index will be very helpful to the reader as well.

Despite the "how to" focus of the book, I find the text is not that easy to understand, and it refers the reader too often all over the book. So from my experience, I suspect that most managers will not really read it, nor fully understand all relevant (statistical) details; the mathematical codes alone take up an Appendix. The book on how to link PVAs with Geographic Information Systems (GIS) still waits to be written.

In either case, I admire in this book that is promotes an overall quantitative approach to wildlife conservation, and specifically I love the last chapters, e.g. Management with Uncertainity, Multiple Site PVAs, Viability-Analysis for Spatially Structured Populations and When and When Not to Perform a PVA (a great argumentation help when doing PVAs). There just is no escape from numbers and reliability in this important conservation field.

This important book makes it clear that well-designed demographical studies and PVAs are nowadays among the basics for any wildlife population to be studied and managed. It provides crucial tools for a quantitative wildlife monitoring and conservation in the new millienium. Now it's once more up to the managers to read, to understand, and fully implement all relevant lessons learnt from this baseline publication.

FALK HUETTMANN

Biology and Wildlife Department, University of Alaska, Fairbanks, Alaska 99775-7000 USA

MISCELLANEOUS

A Bird in the Bush: The Story of the Province of Quebec Society for the Protection of Birds 1917-2002

By Margaret Pye Arnaudin. 2002. Price-Patterson Ltd., Westmount, Quebec. 256 pages. $35 (includes postage). Available from: PQSPB, 111 Elm, Beaconsfield, Quebec H9X 2P5.

The Province of Quebec Society for the Protection of Birds (PQSPB) commissioned this history to celebrate their 85th Anniversary. From the beginning, there was a close connection between the Society, *The Canadian Field-Naturalist* (before 1919, titled *The Ottawa Naturalist*) and members of the Ottawa Field-Naturalists' Club, with which the PQSPB affiliated. The impetus for the PQSPB founding came from the Migratory Birds Convention Act of 1916 and one of the aims of the PQSPB was to provide assistance in carrying out the provisions of the Act. The early members were well connected and used their social contacts to further their cause of conservation. Mount Royal Park and the two Mount Royal Cemeteries were declared bird sanctuaries in 1917 and the Quebec government established bird sanctuaries in the Magdalen Islands, the Gaspe and the Lower North Shore in the early 1920s after petitions by the PQSPB and others. Lewis McIver Terrill was the first president, influential scientist, and a key member from 1917 to 1953. Another very effective president was V. C. Wynne-Edwards (president from 1936 to 1942). Women played a very significant role in the club from the beginning and have always been members of the board. Mrs. Christine Henderson was the first woman president, in 1933.

For over 20 years from 1926 the Education Committee, who were mostly women, organized an Annual

Lecture for Montreal schoolchildren. They were made junior members of the PQSPB and pledged to protect birds. It is estimated that about 50 000 children were "indoctrinated" and made aware of the importance of birds to the natural world. Who knows how influential these lectures were on those young people in later life?

Through the years, the PQSPB board has worked to protect birds and habitat in Quebec, often successfully. However, today collaboration with larger organizations such as The Nature Conservancy is necessary in order to be effective, and many of the early Montreal area sanctuaries have been overwhelmed by development. Other sanctuaries in the rest of Quebec have survived, and there are occasional additions. Many well-known naturalists, scientists and "birdy people" have been associated with PQSPB throughout its history and there will be many Canadians who will be interested in reading about their contribution to bird protection.

JANE ATKINSON

255 Malcolm Circle, Dorval, Quebec H9S 1T6 Canada

Farley: The Life of Farley Mowat

By James King. 2002. Harper Flamingo Canada. xvii + 398 pages.

To paraphrase a legendary literary review of a scholarly book on penguins: "This book tells us more about Farley Mowat than we ever wanted to know". Mowat, a legendary nature chronicler and environmental activist of our time, is depicted in personal detail from cradle to aged guru in great personal detail, not sparing us his relations with two wives, librarian father, mother, and father's mistress/second wife. The publisher assures us, and it is certainly evident in the intimate text, that author King had "unprecedented access" to Mowat, his family, other relatives, editors (notably the legendary Canadian publisher Jack McClelland, the subject of another biography by King), and others.

Mowat was born 12 May 1921. In 2001 there were, according to biographer King's text (page 337), over 460 translations of Mowat's work in 24 languages. In all, Mowat has authored 32 books, been editor for four others, and two collections of his work have been edited by others. Among his writings are his glimpse of Canada's "eskimos" (Inuit) in *People of the Deer* (1952), predators in *Never Cry Wolf* (1963), the Siberian arctic in *Sibir* (1970), cetaceans in *A Whale for the Killing* (1972), the fisheries of the Atlantic in *Sea of Slaughter* (1984), as well as personal accounts of a favourite pet in *The Dog Who Wouldn't Be* (1957), vivid impressions of military service in the Second World War in *And No Birds Sang* (1979), and his own youth in *Born Naked* (1993), and the land *Alive in a Strange Place: A Journey through the Canadian North* (2002) [in King's list; published as *High Latitudes: A Journey*].

King has presented us with a marvellously enthusiastic portrait of the self-made Mowatt. As a self-appointed spokesman on behalf of endangered native people, northern mammals, and marine life, Mowat holds a uniquely prominent, but always controversial, place among popularizers of natural history. He ranks as a equal with the commercially successful fiction and non-fiction authors who brought Canadian literature to world attention over the last half of the 20th Century, but in which category has often been hotly debated. His biographer argues, reflecting Mowat's own view, that in the broad sense Mowat writes the truth, even though he may not strictly follow facts. His concentration is focused on holding the readers' attention with a good story. Mowat is not unique in this. Canada has had other popular natural history writers who effectively promoted public sympathy for the environment and support for its conservation, even the legendary Ernest Thompson Seton himself, who have been suspect of some fudging in their accounts to serve a purpose.

Regrettably, King has apparently not grasped the legitimate concern that truth can be substantiated only through high standards of factual reporting. Nor has he acknowledged the credibility due to members of the mainstream scientific community who adhere to this principle. Here, they are often dismissed, detractors whose views the crusading Mowat was forced to wage a lifelong battle to surmount. However, the real tragedy of Mowat is overlooked. His great writing flair and sincere concern for the environment would likely have made his books as popular even if he had stuck to the facts; that he did not lessened their effectiveness because, whatever the truth in his crusades, they could be dismissed too easily on the basis of his errors. Typical were the comments of Fisheries and Oceans research scientist, David Sergeant, who said in a 1986 review of *Sea of Slaughter* (*Canadian Field-Naturalist* 100(1): 143-144): "Farley's story is packed with interesting facts. The trouble is, many of them don't hold up to critical scrutiny ... Farley's chief fault is sheer exaggeration."

Mowat often increased the scientific negativity toward himself by taunting his detractors. Erling Porsild (1901-1977) who wrote a scathing review of an early book, *People of the Deer*, is summarily dismissed by biographer King as "a civil servant in the Department of Natural Resources and Development". In fact, he was a distinguished arctic field botanist and head of the National Herbarium (scientific plant collection) at the National Museum of Canada (see tribute in *The Canadian Field-Naturalist* 92(3): 298-304). Porsild once told me that some time after his review appeared he received a telegram from Mowat quoting figures to show how much the attention it had brought had increased the sales of the book. It further

informed Porsild that Mowat would be visiting Ottawa and would be at the Bytown Tavern between certain times on a certain date when he would be pleased to autograph Porsild's copy of the book in appreciation. Though Porsild passed up the opportunity, years later he still recoiled at the memory.

A. W. Frank Banfield, once Mowat's field buddy in his student days, is made out as another villain. Banfield, in fact, had not fired his old chum Mowat on his own, but had been forced to by order of his seniors in the Canadian Wildlife Service who were exasperated by Mowat spending government money without authorization, leaving his field work without due notice, and further by giving press conferences when away from his duties. Banfield's later review of *Never Cry Wolf* (1964 *The Canadian Field-Naturalist* 78(1): 52-54) was based on first-hand knowledge as the supervisor of the two-team field party, one team of which had Andrew Lawrie, a graduate biologist in charge, paired with Mowat. Mowat had loosely based the book on this experience but portrayed himself as alone. Frank (by the time of his review Chief Zoologist for the National Museum of Canada, soon to become its Director) had carefully searched the Canadian Wildlife archives to compare Mowat's account and his own memory of events with the historic record before writing his classic critique. When Mowat's reaction to the review came in the mail to him the form of a Letter to the Editor purportedly composed by one of the study wolves, Uncle Albert, Frank passed it over to the journal. "What should we do with this?" he asked. "It's addressed to the Editor of the CFN", I replied. "We publish it of course." And we did (1964 *The Canadian Field-Naturalist* 78(3): 206). Perhaps Mowat has never appreciated how many fans he really had, even among those who had to criticise him for his extravagances.

Mowat had initially started out, as have a legion of scientists-in-training, with an early paper accepted by *The Canadian Field-Naturalist* (1947 "Notes on the birds of Emma Lake, Saskatchewan" 61(3): 105-115). This, his first published writing aside from nature columns for the Saskatoon newspaper, was a careful documentation of his bird observations on part of a field expedition in the summer of 1939, taken jointly with then fellow University of Toronto student Banfield (the latter published in 1941 on Saskatchewan mammals taken on the same expedition: *The Canadian Field-Naturalist* 55(8): 117-123). Both served in the Canadian forces in World War II, and, when it concluded, were reunited for the Caribou-Wolf study then being initiated by the Canadian Wildlife Service. After that, their subsequent career tracks in natural history in Canada could hardly have diverged more.

FRANCIS R. COOK

RR 3, North Augusta, Ontario K0G 1R0 Canada

NEW TITLES

Zoology

Account of the collection of marine shells. 2003. By W. Judd. Phelps Publishing Co., London, Ontario. 38 pages.

***Attu: Birding on the edge**. 2003. Edited by C. Walters. American Birding Association, Colorado Springs, Colorado. 213 pages., illustrated. U.S. $35, paper.

Belugas in the North Atlantic and the Russian Arctic. 2002. Edited by Mads Peter Heide-Jourgensen and Oystein Wiig. Nammco Scientific Publications. Volume 4. 270 pages, illustrated Norwegian Kroner. Canadian $30.

Beaver tales. 2003. Audrey Tournay. The Boston Mills Press. 157 pages, illustrated. U.S. $14.95. Canadian $19.95.

Birds of Nebraska; their distribution and temporal occurrence. 2003. By Sharpe, Silcock and Jorgenson. University of Nebraska Press, Lincoln. 2001. pages illustrated. U.S. $69.95 cloth.

Birds of the Yukon Territory. 2003. Edited by P. Sinclair, W. Nixon, C. Eckert and N. Hughes. University of British Columbia Press, Vancouver, B.C. 596 pages, illustrated. Canadian $125.00.

Birds of the West Indies. By H. Raffaele. J. Wiley, O. Garrido, A. Keith and J . Raffaele., 2003. Princeton University Press, Princton, New Jersey. U.S. $24.95.

Birding on borrowed time. 2003. By Phoebe Snetsinger. American Birding Association. 307 pages, illustrated. U.S. $19.95.

Bugs of Ontario. 2003. By John Acorn, and Ian Sheldon. Lone Pine Publishing. 160 pages, illustrated. Canadian $14.95.

* **Built for Speed:** *A year in the life of a Pronghorn.* 2003. By John Byers. Harvard University Press. 230 pages, illustrated. U.S. $24.95 cloth.

Dictionary of Birds of the United States: Scientific and common Names. 2003. By Joel E. Holloway. Illustrations by George Miksch Sutton. Timber Press, Inc., Portland, Oregon. U.S. $19.95.

For the love of insects. 2003. By T. Eisner. Harvard University Press, Cambridge, Massachusetts. 448 pages, illustrated. U.S. $29.95 paper

* **The Firefly encyclopedia of Birds**. 2003. Edited by Christopher Perrins. Firefly Books Ltd., Toronto, Ontario 640 pages, illustrated. $75 Canadian.

Fish of Alberta. 2003. By A. Joynt and M. Sullivan. Lone Pine Publishing, Edmonton, Alberta. 176 pages, illustrated. Canadian $18.95.

* **Guide to the reptiles of the eastern Palearctic**. 2003. By N. N. Szczerbak. Krieger Publishing Company, Florida. U.S. $73.50

* **Handbook of birds of the world**. 2003. Volume 8 Broadbills to Tapaculos. Edited by Josep del Hoyo, Andrew Elliott and Jordi Sargatal. Lynx Edicions, Barcelona, Spain. 850 pages, illustrated. U.S. $195. Cloth.

* **Important bird areas in Africa and associated islands**. 2001. Edited by D. Lincoln, C. Fishpool, and Michael I. Evans. Pisces Publications and Bird Life International. 1144 pages, illustrated. U.S. $82.50.

Orb weaving spiders of Canada and Alaska. 2003. By C. Dondale, J. Redner, P. Paquin, and H. Levi. National Research Council Press, Ottawa, Ontario. 371 pages, Illustrated. Canadian $42.95 paper.

* **Pete Dunne on bird watching**. 2003. By Pete Dunne. Houghton Mifflin Company. Boston. 334 pages., illustrated. U.S. $12.

Reptiles of Australia. By S. Wilson and Gerry Swan. 2003. Princeton University Press, Princeton, New Jersey. 48 pages, illustrated. U.S. $29.95 paper.

Seven names for the bellbird. 2003. By M. Bonta. Texas A & M Press, Texas. Illustrated, U.S. $35.00.

* **Sharks.** 2003. By A. and A. Ferrari. Firefly Books. U.S. $24.95.

Snakes and their ways. .2003 [Original edition 1937]. By H. Curran and C. Kauffeld. 305 pages. Krieger Publishing, Melbourne, Florida. U.S. $39.50. Cloth.

***Snakes of the United States and Canada: natural history and care in captivity.** By John V. Rossi and Roxanne Rossi. 2003. Krieger Publishing, Florida.

Snakes of the Americas: checklist and lexicon of common names. By Bob L. Tipton. Krieger Publishing, Melbourne, Florida. Price not set.

True vipers: natural history and toxinology of Old World vipers. 2003. By David Mallow, David Ludwig, and Göran Nilson. Krieger Publishing, Florida. U.S. $79.50.

* **The wind masters**. 2003. By Pete Dunne. Houghton Mifflin Company, Boston. 263 pages, illustration. U.S. $14.00.

Botany

Botanical Latin (4th Edition). 2004. By W. Stearn. Timber Press, Portland, Oregon. 560 pages, illustrated. about U.S. $40.

* **Edible and poisonous mushrooms of the world**. 2003. By I. Hall, S. Stephenson, P. Buchanan, W. Yun and A Cole. Timber Press, Portland, Oregon. 372 pages, illustrated. U.S. $54.95 cloth.

The Facts on File Dictionary of botany. 2003. By J. Bailey. Checkmark Books, N.Y., N.Y. 250 pages, illustrated, U.S.$199.95.

* **Flora of the Hudson Bay Lowlands and its post glacial origins**. 2003. By John Riley. National Research Council Press, Ottawa, Ontario. Canadian $49.95.

Native Trees for North American landscapes. 2004. By Guy Sternberg with Jim Wilson. Timber Press, Portland, Oregon. 552 pages. illustrated. U.S. $59.

The orchid in lore and legend. 2004. By L. Berliocchi. Timber Press, Portland, Oregon. 200 pages, illustrated. U.S. $27.95

***Pondweeds, bur-reeds and their relatives of British Columbia**. 2000. By T. Christopher, Brayshaw. Royal British Columbia Museum, Victoria, B.C. illustrated. Canadian $24.95.

Tropical flowering plants: a guide to identification and cultivation. 2003. By Kirsten Albrecht Liamas. Timber Press, Inc., Portland, Oregon. U.S. $95 cloth.

* **Wild flowers of forest and woodland in the Pacific Northwest**. 2003. Edited by John G. S. Trelawny. Harbour Publishing. 100 pages, illustrated. Canadian $12.95.

* **Wild flowers of the mountains of the Pacific Northwest**. 2003. Edited by John G. S. Trelawny. Harbour Publishing. 106 pages, illustrated. Canadian $12.95.

***Wild flowers of the Yukon, Alaska and Northwestern Canada**. 2nd Edition. 2003. By John G. Trelawny. Harbour Publishing. 224 pages, illustrated. Canadian $24.95.

Environment

* **Amazonia.** 2003 By A. Capelas Jr. Firefly Books Ltd., Willowdale, Ontario. 160 pages, illustrated. Canadian $35.00.

Antarctica. 2003. By D. McGonigal and L. Woodworth. Firefly Books Ltd., Willowdale, Ontario 224 pages, illustrated. Canadian $39.95.

† **Democracy's Dilemma.** 2003. By Robert C. Paehlke. The MIT Press, Cambridge, Massachusetts. 306 pages. U.S. $27.95.

Globalization and Environmental reform. 2003. By P. Mol. MIT Press, Cambridge, Massachusetts. 299 pages, illustrated, U.S. $24.95.

† **The importance of species.** 2003. By T. P. Kariva and S. Levin. Princeton University Press, Princeton, New Jersey 427 pages. U.S. $35.00 paper.

Journey into the Arctic. 2003. By B. and C. Alexander, Oxford University Press, Oxford, UK. 49 pages, illustrated. $19.95 paper.

Nature by design. 2003. By E. Higgs. MIT Press, Cambridge, Massachusetts. 341 pages, illustrated, U.S. $27.95.

* **A passion for wildlife**. 2003. By J. Alexander Burnett. UBC Press. Vancouver. 331 pp., illus. Canadian. $27.95 paper, $85.00 cloth.

Rivers for life: managing water for people and nature,. 2003. By Sandra Postel and Brian Richter. Island Press, Washington, D.C. U.S. $25.00.

† **Visions of the land**. 2002. By Michael A. Bryson. University Press of Virginia. 228 pages, U.S. Cloth $45.00, Paper $16.50

* **When the wild comes leaping up**. 2002. Edited by David Suzuki. Greystone Books, Vancouver. 234 pages, Canadian $22.95.

Miscellaneous

***Canoeing and hiking wild Muskoka**. 2003. By Hap Wilson. The Boston Mills Press. 144 pages, illustration. Canadian $19.95.

***An intimate look at the night sky.** 2003. By Chet Raymo. Greystone Books. 242 pages, illustrated. Canadian $24.95.

Inventing for the environment. 2003. Edited by Molella A. and J. Bedi. MIT Press. 5 Cambridge Center, Cambridge, Massachusetts. 398 pages, illustrated. $29.95 U.S. cloth.

***National Audubon Society guide to nature photography**. 2003. By Tim Fitzharris. Firefly Books Ltd., Toronto, Ontario. 192 pages, illustrated, Canadian $29.95 paper, $35 cloth.

Ecology for Gardeners. May 2004. By Steven B. Carroll and Steven D. Salt. Timber Press, Portland, Oregon 97204, USA. 420 pages, illustrated, U.S. $29.95 cloth.

The Lewis and Clark Columbia River water trail: a guide for paddlers, hikers, and other explorers. 2004. By Keith G. Hay. Timber Press, Portland, Oregon 260 pages, illustrated. U.S. $19.95.

***The north runner**. 2003. By R. D. Lawrence. Natural Heritage Books, P.O. Box 95 Station O Toronto, Ontario. illustrated. Canadian $22.95.

Towards sustainable management of the boreal forest. 2003. Edited by P. Burton, C. Messier, D Smith and W. Adamowicz. 1039 pages. Canadian $69.95.

Wildlife conservation and human welfare – US and Central Canadian perspective. 2003. By R. D. Taber and Neil Payne. Krieger Publishing Company, Malabar, Florida. 218 pages. U.S. $29.50 paper.

Writing on air. 2003. By D. Rothenburg and W. Pryor MIT Press, Cambridge, Massachusetts. 322 pages, illustrated. U.S. $29.95 cloth.

Books for Young Naturalists

Mammals. 2003. P. Morris and A. Beer. Grolier. 128 pages, illustrated. U.S. $ 419.00 (Set of 10 volumes)

Rachel Carson: Author/Ecologist. 2003. E. Tremblay. Chelsea House, Broomall, PA. 118 pages, U.S. 22.95.

† Available
*Assigned

News and Comment

Point Pelee Natural History News 3(2)

The summmer 2003 issue, volume 3, number 2, pages 21-36, contains: White-faced Ibis: New to Point Pelee (Alan Wormington) — Noteworthy Bird Records: March to May 2003 — (Alan Wormington) — White-winged Dove: New to Essex County (Stuart A. Mackenzie) — In the Field [Pileated Woodpecker; Hermit Warbler; Swallows grounded; Red-throated Loon] — Upcoming Events and Outings.

This newsletter for Point Pelee National Park, Ontario, is published by the Friends of Point Pelee and edited by Alan Wormington (e-mail: wormington@juno.com). Editorial Assistants are Gordon D. Harvey and Michelle T. Nicholson. The web site is www.wincom.net/~fopp/Natural_History_News.htm. Subscription rates are Canada: CAN $20 (one year) or $40 (two years); International: US $20 (one year) or $40 (two years). Send payment (and e-mail address, optional) to The Friends of Point Pelee, 1118 Point Pelee Drive, Leamington, Ontario N8H 3V4 Canada. Issues are mailed in March, June, September, and December. Back issues of volumes 1 and 2 are available for $15 per Volume/ $5 per single issue.

Canadian Species at Risk May 2003

Issued by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), the list is 43 pages containing: About COSEWIC (mandate, membership, definitions) — Summary Tables (COSEWIC species designated in five "risk" categories and in Not at Risk, and Data Deficient categories (Tables 1-3), — Results of May 2003 COSEWIC meeting (Tables 4-5) — COSEWIC Assessment Results — Explanation of symbols — Species examined in five "risk" categories (Table 6), Not at Risk (Table 7), and Data Deficient (Table 8) — Record of Status Re-examinations — Record of Name Changes. Listed now are 12 extinct, 21 extirpated, 153 endangered, 102 threatened, and 143 of special concern. Of the 431 forms in these categories, 64 are mammals, 56 birds, 31 reptiles, 19 amphibians, 807 fishes, 13 lepidopterans, 18 molluscs, 136 vascular plants, 8 mossses, and 6 lichens. In addition 152 forms have been considered and found not at risk, and 29 to be data deficient.

This publication is available from COSEWIC Secretariat, Canadian Wildlife Service, Environment Canada, Ottawa, Ontario K1A 0H3. See Web site: http://www.cosewic.gc.ca.

Marine Turtle Newsletter (101)

July 2003. 56 pages: ARTICLES: Sea Turtles in Spanish Mediterranean Waters: Surprises in 2001 — Confirmed Leatherback Turtle (*Dermochelys coriacea*) nests from North Carolina, with a summary of Leatherback nesting activities north of Florida — Monitoring nesting Loggerhead Turtles (*Caretta caretta*) in the central Caribbean Coast of Colombia — Incidental capture of Loggerhead Turtles (*Caretta caretta*) on Boa Vista (Cape Verde Islands) — Observations on Sea Turtles in the state of of Paraiba, Brazil — Epibiotic associates of ocean-stage Loggerhead Turtles from the southeastern North Atlantic — NOTES: The first report of oral tumors associated with fibropapillomatosis in Florida, USA — The first records of Olive Ridleys in Florida, USA — Olive Ridley Sea Turtles in Porto-Novo, Tamil Nadu, India, with an observation of an Asian Giant Softshell Turtle — Green Turtle with living tag captured in the southern Bahamas — Second record of a Green Turtle (*Chelonia mydas*) tagged in Brazil and captured in Nicaragua — When a turtle is worth a hook — Possible factors leading to non-occurrence of 'Arribada' at Gahirmatha, Orissa, India in 2001-2002 — MEETING REPORTS — BOOK REVIEWS — ANNOUNCEMENTS — NEWS & LEGAL BRIEFS — RECENT PUBLICATIONS.

The Marine Turtle Newsletter is edited by Brendan J. Godley and Annette C. Broderick, Marine Turtle Research Group, School of Biological Sciences, University of Wales, Swansea, SA2 8PP Wales, United Kingdom; e-mail MTN@swan.ac.uk; Fax +44 1792 295447. Subscriptions to the MTN and donations towards the production of MTN and its Spanish edition NTM [Noticiero de Tortugas Marinas] should be made online at http://www.seaturtle.org/ntm/ or c/o SEATURTLE.ORG 11400 Classical Lane, Silver Spring, Maryland 20901 USA.

Froglog: Newsletter of the Declining Amphibian Populations Task Force (58)

Number 58, August 2003. Contents: Status of Amphibians at the Zoige Wetlands, Sichuan Province, China (Gary M. Fellers, Wang Yuezhao, and Liu Shaoyin) — DAPTF Seed Grants 2004 (Tim Halliday) — Gren Frogs are Greatly Endangered in Serbia and Montenegro (Katarina Ljubisavljevic, Georg Dzukic & Milos Kalezic) — Amphibian Monitoring Standards: a Workshop for African Students (Stefan Lotters) — Amphibians in Guatemalan Pine-Oak Forests (Daniel Ariano Sanchez and Alejandro Del Valle Moreno) — DAPTF — Kenya Working Group: Review of Activities June 2002 — June 2003 (Damaris Rotich) — Froglog Shorts.

Froglog is the bi-monthly newsletter of the Declining Amphibian Populations Task Force of The World Conservation Union (IUCN)/Species Survival Commission (SSC) and is supported by The Open University, The World Congress of Herpetology, and Arizona State University. The newsletter is Edited by John W. Wilkinson, Department of Biological Sciences, The Open University, Walton Hall, Milton Keynes, MK7 6AA, United Kingdom; e-mail: daptf@open.ac.uk. Funding for *Froglog* is underwritten by the Detroit Zoological Institute, P. O. Box 39, Royal Oak, Michigan 48068-0039, USA. Publication of issue 58 was also supported by Peace Frogs www.peacefrogs.com and by RANA and the US National Science Foundation grant DEB-0130273.

Minutes of the 124th Annual Business Meeting of The Ottawa Field-Naturalists' Club 14 January 2003

Place and time: Victoria Memorial Building, Canadian Museum of Nature, Ottawa, Ontario, 7:30 pm
Chairperson: Eleanor Zurbrigg, President
Attendance: Forty-four persons attended the meeting.

Attendees spent the first half-hour reviewing the minutes of the previous meeting, the Treasurer's report and the Report of Council. The meeting was called to order at 7:35 pm with some opening remarks from Eleanor Zurbrigg, the President.

1. Minutes of the Previous Meeting

Under the report of the Nominating Committee, Ron Bedford's name was mispelled.

It was moved by Roy John and seconded by Diane Lepage, that the minutes be accepted as amended.

(Motion Carried)

2. Business Arising from the Minutes

We are not receiving the annual reports from the Trinidad and Tobago Naturalists' Club, although we are getting their newsletters.

Concerning the Soiree, both the Excursions and Lectures Committee and the Education and Publicity Committee are working on re-vamping the Soiree.

3. Communications Relating to the Annual Business Meeting

There were no communications relating to the Annual Business Meeting.

4. Treasurer's Report

Frank Pope reviewed the financial report for the year ending September 30, 2002, noting that the Club's net assets had increased by $38,274. As a result of the fund-raising campaign begun in April, 2002, the OFNC was able to send $55,000 to the Nature Conservancy to help with the purchase of land in the Alfred Bog. The Club also contributed $1000 to the Nature Conservancy toward the purchase of the Cameron Ranch in the Carden alvar.

Moved by Frank Pope and seconded by Ron Bedford that the Financial Report be accepted. (Motion Carried)

5. Committee Reports

Eleanor Zurbrigg introduced each of the Committee reports and a representative of the appropriate Committee and asked for questions and comments. She thanked the committee chairs and committee members for their work over the past year. She also mentioned that Frank Pope and Bill Cody each received Queen's Jubilee medals this year.

Moved by Dave Hobden, seconded by Roy John, that the reports as amended be accepted. (Motion Carried)

6. Nomination of the Auditor

Moved by Frank Pope, seconded by Bill Cody, that Janet Gehr continue as Auditor for another year. (Motion Carried)

7. Report of the Nominating Committee

Fenja Brodo expressed thanks to Eleanor Zurbrigg (President), Roy John (Vice-President) and the rest of Council on behalf of the club.

President	Garry McNulty
Vice President	Mike Murphy
Vice President	Gillian Marston
Secretary	Susan Laurie Bourque
Treasurer	Frank Pope
Past President	Eleanor Zurbrigg
Business Manager	Bill Cody
Editor, CFN	Francis Cook
Editor, T&L	Karen McLachlan Hamilton

Committee Chairs

Birds	Chris Traynor
Computers	Janet Castle
Conservation	Stan Rosenbaum
E&P	John Cameron
E&L	Roy John
Finance	Louise Schwartz
FWG	David Hobden
Macoun rep	Barbara Gaertner
Membership	Dave Smythe
Publications	Ron Bedford
FON Rep	Cendrine Huemer

Members at large

Charlie Clifford
Kathy Conlan
Marcel Gahbauer
Diane Lepage

Chairs not on Council

Awards	Ernie Brodo
Macoun	Rob Lee
Nominations	Fenja Brodo

Retiring from the Council: Allison, Moore, McBride, Roach, Goddard, Holmes

New on the Council: Castle, Traynor, Huemer, Murphy, Bourque, Gahbauer

Moved by Fenja Brodo, seconded by Frank Pope, that the slate of nominations for the 2003 Council be accepted.

(Motion Carried)

8. New Business

There was no new business.

9. Presentation by the Excursions and Lectures Committee

Roy John and Philip Martin gave an often-humorous presentation on their experiences on field trips over the years. Roy mentioned that the Committee is always looking for speakers and trip leaders, as well as suggestions for trips and

topics. If you are interested in volunteering, please contact Roy John.

10. Adjournment

Moved by Diane Lepage, seconded by Lee Cairney that the meeting be adjourned at 9:20 pm.

(Motion Carried)

KEN ALLISON
Recording Secretary

The Ottawa Field-Naturalists' Club Committee Reports for 2002

Alfred Bog Fund Raising Ad Hoc Committee

The Committee was formed after the Nature Conservancy of Canada announced that it had taken an option to purchase 3000 acres in Alfred Bog. The purchase price was $2,500,000 the cost to be shared equally by the Federal Government, Ontario government and private donations. Most of the funds raised by the Committee came from an appeal to the members in a letter from President Eleanor Zurbrigg. The option was taken up by the Nature Conservancy in October but a loan was required to reach the full amount. The Committee then disbanded. I am pleased to report that in the first week of October the OFNC contributed $55,000 toward the purchase.

FRANK POPE

Awards Committee

The Awards Committee met in January to consider nominations made for the various OFNC Awards. During the following weeks and months, numerous communications were held by e-mail and Canada Post as well as by phone. As a result of our deliberations, the following awards for the year 2001 were presented at the OFNC's Annual Soirée, which took place 26 April 2002.

HONORARY MEMBER

Dr. John B. Theberge: for his ecological studies of wolves, his work in establishing parks, and outsanding books on Canadian natural history.

MEMBER OF THE YEAR

Eve D. Ticknor: for her work on Falcon Watch as well as other birding activities of special importance.

GEORGE MCGEE SERVICE AWARD

Fenja Brodo: for her ten years of serving as an outstanding editor of *Trail & Landscape.*

ANNE HANES NATURAL HISTORY AWARD

Robert Bracken and Christina Lewis: for their remarkable studies and publications on the dragonflies and damselflies of the Ottawa Region.

CONSERVATION AWARD – MEMBER

David White: for his important studies of the vascular plants of the Ottawa Region leading to the preservation of ecologically sensitive lands.

CONSERVATION AWARD – NON-MEMBER

The Land Preservation Society of the Ottawa Valley (and presented to their President, Marc Stabb): for the Society's unrelenting and ultimately successful struggle to save Gillies Grove, a magnificent old growth forest in Arnprior.

The Committee also dealt with a few other community awards on behalf of the OFNC, including the Golden Jubilee Medal nominations in July, 2002. Our nomination resulted in a medal being given to E. Franklin Pope for his many and varied services to the Ottawa Field-Naturalists' Club over many years.

I. BRODO

Birds Committee

The Birds Committee participated jointly with the Club des Ornithologues de l'Outaouais to run successful Christmas Bird Counts at the end of 2001. Plans are in place for 2002 counts. We also had a well-attended fall bird count in October 2002. We ran the Peregrine Falcon Watch at the downtown Ottawa nest site, which attracted many volunteers and club members. We anticipate running a watch in 2003. The Bird Records Sub-committee met during the year to review records of rare birds for the area. Results of their work will appear in an upcoming *Trail & Landscape*. Representing a culmination of hard work for the sub-committee, we are about to publish a revised version of the former, popular "blue checklist" for recording bird species seen in the field in the Ottawa 50 km circle. The second year of surveying for the Ontario Breeding Bird Atlas 2nd edition was a great success with all our region's squares being covered by an eager team of volunteers. Our seed-a-thon raised around $850.00 for the club's bird feeders, which continue to be popular for both birds and humans. Our bird study group held several sessions during the year which were well-attended. In 2002 for the first time we combined an indoor session with an outdoor field trip, to practice identifying waterfowl from a distance. We continue to operate the rare bird alert telephone tree and the Ottawa Bird Status Line, which is a recorded telephone message providing current bird sightings. In 2002 we upgraded the status line to a more technologically appropriate telephone system.

B. MCBRIDE

Computer Management Committee

No report.

Conservation Committee

Appearances at hearings:

The committee represented the OFNC at meetings of the City of Ottawa Planning and Development Committee on (1) Leitrim Wetland zoning revisions for development, (2) Preliminary Draft Official Plan.

Frank Pope will speak in support on 18 November 2002 at a special tribunal on Alfred Bog, regarding requirement for Water Taking Permits.

Brittania Greening Project (at Brittania Water Filtration Plant):

A site plan is being prepared by the City. Cooperation between City staff, consultant Dan Brunton, OFNC (Diane Holmes, Christine Hanrahan) and the Regina Street School will put emphasis on native species for compatibility with adjoining significant wetlands and woodlands.

Appointments to study/ focus groups:

Kathy Conlan is representing the OFNC at the Lower Rideau Watershed Study Community Focus Group 16-month study.

Bill Royds is representing the OFNC at the Sawmill Creek Watershed Study (about 1 km north of Leitrim wetlands).

Richmond Conservation Area Management Team:

Our re-nomination of Robert Marler was rejected because we declined to submit the names of two nominees. The new rules were applied to all nominations, but were quite obviously set up to allow the City to reject a certain individual (not the OFNC nominee).

Donations from OFNC (other than Alfred Bog Fund expenses):

$1,000 was contributed in late 2001 or early 2002 to Lac Leamy Coalition (a Quebec group named CREDDO) in support of stopping a golf course on NCC land adjacent to these significant wetlands. (Golf course was stopped);

$1,000 was contributed to the Nature Conservancy of Canada in support of acquiring Carden Alvar.

A few of the other meetings attended by CC members included: City of Ottawa Environment Committee Workshop, NCC Workshop on Mer Bleue, Ottawa Forests Advisory Committee Workshop, Natural Sports Turf (Larry Pegg) two meetings.

Alfred Bog Fund

Contributions made via OFNC for this fund reached $52,500 by early October, from 257 donations. Overall contributions (including from OFNC donors) to Nature Conservancy of Canada reached about $620,000, leaving a shortfall of about $200,000 still to be raised.

S. ROSENBAUM

Education and Publicity Committee

1. Following one of the suggestions in the Carleton University Students' Communications Plan, a new design for the membership brochure was developed with the help of Theo van Ulft of Van Ulft Designs. One thousand new brochures were printed by Photoset Group, Canotek Road, in June 2002. These brochures are being more widely distributed in museums and nature stores.
2. With the help of 16 volunteer OFNC members, the Committee staffed the OFNC booth at the Carlingwood Wildlife Festival, April 12-14.
3. The Ottawa Field-Naturalists' Club presents 3 Natural History Awards annually at the Ottawa Regional Science Fair. The awards consist of a cash prize of $50.00 and a one-year membership in the Club. The Committee finds judges for this event, who this year were Dr. Kathy Conlan and Stan Rosenbaum.
4. The Committee staffed a booth at the annual meeting of the Canadian Nature Federation at Carleton University in June. Although the booth was downstairs from the registration area, there was good interest shown by the delegates.
5. OFNC booths were staffed at a variety of events such as Earth Day, Sparks Street Mall, and the Richmond Fair.
6. From the proceeds of the Sale Table, $300.00 was given to the Club, and $58.00 was given to the Alfred Bog Fund.

P. PETERKIN

Excursions and Lectures Committee

The Excursions & Lectures committee (E&L) organized 9 evening sessions, the annual general meeting and 24 field trips, including one bus trip. In addition, the club held its annual soiree and awards presentation night. The OFNC joined the Canadian Nature Federation in preparing for the CNF AGM held in Ottawa. The E&L committee formed a special group headed by John Bennet and Irwin Brodo to organize the field trips for this conference. As we were tumbled into this project very late in the year the club owes these two people and those that supported them a strong vote of thanks. Not only did they work rapidly and diligently, they produced an excellent program. I have expressed my concern to the CNF Director about the lack of time for preparation and the split responsibilities that resulted.

Through the Education and Publicity Committee E&L received a Carleton University Student report on our activities. This report reviewed our program and made comments and suggestions. The E&L Committee has evaluated the report and we are taking action on the ideas presented and number of suggestions spawned by the report.

During the year Carleton Bus Lines, an organization we have dealt with for many years, went out of business. We have now made similar arrangements with Thom Bus Lines to provide a similar service and this is working well.

During the year some E&L members resigned and we have recruited three new people as replacements. One of these people, Phil Jeffries, has taken on the soiree as a special project and is making excellent progress. The club has now re-established its link with the tour operator in Leamington and will be running its traditional spring trip to Point Pelee in the spring.

R. JOHN

Executive Committee

The Executive Committee has not met in the past year.

E. ZURBRIGG

Finance Committee

The Committee reviewed the 2001-2 financial statement before it was presented to Council and the Annual Business Meeting. In March it considered dues for 2003 and advised the Council to make no changes. In September, the Chair tabled a draft budget for 2002-3 which was approved for the October meeting of the Council. During the year, the Committee advised the Council on the financial implications associated with OFNC support for the Taverner Cup competition and fund raising to support the acquisition of 3000 acres in Alfred Bog.

LOUISE SCHWARTZ

Fletcher Wildlife Garden Committee

The Fletcher Wildlife Garden has completed another successful year despite a shortage of leaders for some activities. Volunteers contributed well over 2000 hours of their time. The Management Committee met monthly except in December.

The Bill Holland Trail was improved by doing our own mowing along it. Individual volunteers are looking after specific beds of the backyard garden after the manager stepped down. Invasive plant control is still a problem. The City of Ottawa provided a grant to buy tools to remove buckthorn and plants to replace it. The swallow-wort research project has not provided any magic solutions so the worst areas were mowed in August. Hand pulling of swallow-wort and garlic mustard continued in the Old (Ash) Wood lot. In order to maintain the old field area in an early state of regeneration it was mowed in the Fall. Several young black walnut trees have nuts on them for the first time.

A grant enabled us to have a summer student employee from mid-June to late August. He was able to keep the Interpretation Centre open much of the time and meet visitors as

well as doing outside work and observations. Our web site now contains a series of "fun facts" which he created for junior visitors.

Volunteers also opened the Interpretation Centre on Sunday afternoons from May to October. We had displays at the Wildlife Festival and at the Museum of Nature at the start of the Green Legacy Exhibition. We provided tours for two Museum of Nature activities and an Open House for the Canadian Nature Federation Annual Meeting in June.

Summer 2002 saw some welcome media attention, ranging from an article in local community newspapers to a CBC radio feature and filming for two television programs to be shown on the PBS network and Discovery Channel.

The Taverner Cup was held at the end of May with 14 teams and 58 people participating and OFNC acting as a sponsor. About $3000 was distributed to a variety of ecological causes.

D. HOBDEN

Macoun Field Club Committee

The Committee met only once during the year, rather than every two months as formerly. All planning for the children's weekly meetings was carried out by individuals, rather than the group. As usual, however, Committee members supervised all 48 indoor meetings, and led the 17 field trips and 2 camping trips.

Indoor meetings introduced the children and high-school students to basic matters, like note-keeping, and to issues such as deforestation, developed identification skills through workshops, and explored a variety of natural history topics from around the world.

The field trips enabled members to develop a general familiarity with the region's natural history, and with the natural environment itself as a place to be at home regardless of season and weather. There was a continued focus on two primary destinations: the Macoun Club's nature study area in Stony Swamp, and Mary Stuart's lands in the Pakenham Hills. The one place is for study, the other for exploration.

Macoun members themselves produced a monthly newsletter and published the annual 100-page Little Bear magazine, with minimal supervision. Both Club and Committee members contributed substantially to the Club's web site, which now features accounts of the expert presentations heard at indoor meetings, summaries of study-area research, and updates on former members and leaders.

R. LEE

Membership Committee

The distribution of memberships for 2002 is shown in the table (below), with the comparable numbers for 2001 in brackets. These statistics do not include five complimentary memberships awarded to winners of the 2002 Science Fair competition nor the 23 affiliate organizations which receive copies of the Club's publications.

This year, the Club lost one of its most distinguished members with the death of W. Earl Godfrey, former ornithologist at the Canadian Museum of Nature, and a member and active participant in Club activities since 1947.

D. SMYTHE

Distribution of Memberships in The Ottawa Field-Naturalists' Club

Type	Canadian				Foreign				Total	
	Local		Other		USA		Other			
Family	340	(345)	29	(31)	1	(3)	2	(2)	372	(381)
Individual	345	(366)	120	(121)	26	(22)	5	(4)	496	(513)
Honorary	15	(17)	9	(8)	0	(0)	0	(0)	24	(25)
Life	21	(21)	21	(22)	5	(5)	1	(1)	48	(49)
Sustaining	8	(8)	3	(2)	0	(0)	0	(0)	11	(10)
Total	729	(757)	182	(184)	32	(30)	8	(7)	951	(978)

Publications Committee

The Publications Committee met twice in 2002.

Three issues of *The Canadian Field-Naturalist* were published in 2002: Volume **115**, #3, 4 and Volume **116**, # 1. These three issues contained 558 pages; 31 articles; 19 notes; 18 COSEWIC articles; 57 book reviews; 268 new titles; 1 commemorative tribute; 19 pages of News and Comment; and a 33 page index. Long-time Associate Editor for ornithology, Earl Godfrey, died in June. Two new Associate Editors were appointed: Mr. David Nagorsen (B.C.) (mammals), and Dr. Donald McAlpine (New Brunswick Museum) (several fields). One article qualified for financial support from the Manning Memorial Fund, for a total of nine to date. The publication schedule slipped badly in 2002, falling almost one year behind, causing dissatisfaction for some contributors and adversely affecting the journal's reputation. Steps taken to remedy this situation include getting editorial and proof-reading assistance for the Editor.

Volume 36 of *Trail & Landscape* was published in four issues containing 160 pages with the usual mix of articles. Council was advised of budgeting problems with *T&L* for the past two or three years.

R. BEDFORD

Auditor's Report

To The Members of THE OTTAWA FIELD NATURALISTS' CLUB

I have audited the balance sheet of THE OTTAWA FIELD-NATURALISTS' CLUB as at September 30, 2002, the statement of changes in net assets, and the statements of operations. These financial statements are the responsibility of the organization's management. My responsibility is to express an opinion on these statements based on my audit.

Except as explained in the following paragraph, I conducted my audit in accordance with generally accepted auditing standards. Those standards require that I plan and perform an audit to obtain reasonable assurance whether the financial statements are free of material misstatement. An audit includes examining evidence supporting the amounts and disclosures in the financial statements. An audit also includes assessing the accounting principles used and significant estimates made by management, as well as evaluating the overall financial statement presentation.

In common with many non-profit organizations, the Ottawa Field-Naturalists' Club derives some of its revenue from memberships, donations, and fund raising activities. These revenues are not readily susceptible to complete audit verification, and accordingly, my verification was limited to accounting for the amounts reflected in the records of the organization.

In my opinion, except for the effect of the adjustments, if any, which I might have determined to be necessary had I been able to satisfy myself concerning the completeness of the revenues referred to in the preceding paragraph, these financial statements present fairly, in all material respects, the financial position of the OFNC as at September 30, 2002, and the results of its operations and changes in net assets for the year then ended in accordance with generally accepted accounting principles.

JANET M. GEHR
Chartered Accountant

North Gower, Ontario
January 11, 2003

The Ottawa Field-Naturalists' Club
Balance Sheet
September 30, 2002

	2002	2001
ASSETS		
CURRENT		
Cash (Note 1)	$ 71,087	$ 50,760
Investment certificates (Note 1)	84,790	110,219
Marketable securities (Note 2)	235,758	194,234
Accounts receivable	7,238	5,386
Prepaid expenses	1,000	1,000
	399,873	361,599
CAPITAL ASSETS (Note 3)	–	–
Land – Alfred Bog	3,348	3,348
	$ 403,221	$ 364,947
LIABILITIES AND FUND BALANCES		
CURRENT		
Accounts payable and accrued liabilities	$ 2,000	$ 2,000
Deferred revenue	13,500	13,788
	15,500	15,788
Life memberships	11,721	11,721
NET ASSETS		
Unrestricted	80,325	99,427
Club reserve	100,000	100,000
Manning principal	100,000	100,000
Manning interest - OFNC	1,963	2,186
- CFN	13,179	8,225
Seedathon	2,087	1,569
Anne Hanes memorial	870	870
de Kiriline-Lawrence	23,975	24,553
Macoun Baillie Birdathon	1,327	(7)
Alfred Bog	52,274	615
	376,000	337,438
	$ 403,221	$ 364,947

The Ottawa Field-Naturalists' Club
Statement of Operations
For the Year Ended September 30, 2002

	2002	2001
REVENUE		
Memberships	$ 15,488	$ 15,675
Trail and Landscape	196	266
Interest	1,457	2,203
GST rebate	4,532	–
Other	760	984
	22,433	19,128
OPERATING EXPENSES		
Affiliation fees	680	455
Computer	216	534
Membership	1,437	1,365
Office assistant	1,000	1,000
Telephone	1,848	1,593
Insurance	655	688
Audit	1,000	1,000
GST	1,316	1,505
Other	2,847	782
	10,999	8,922
CLUB ACTIVITY EXPENSES		
Awards	471	280
Birds	223	466
Education and Publicity	1,322	182
Excursions and lectures	164	(311)
Macoun Field Club	1,027	955
Soiree	466	65
Trail and Landscape	9,088	8,794
Fletcher Wildlife Garden (Note 4)	1,294	(2,281)
Other	–	265
	14,055	8,415
	25,054	17,337
EXCESS EXPENSES OVER REVENUE	$ (2,621)	$ 1,791

The Ottawa Field-Naturalists' Club
Canadian Field-Naturalists — Statement Of Operations
For the Year Ended September 30, 2002

	2002	2001
REVENUE		
Memberships	$ 10,325	$ 10,447
Subscriptions	28,483	28,869
Reprints	5,608	10,654
Publication charges	16,812	30,212
Interest and exchange	10,404	17,386
GST rebate	3,448	–
Other	339	330
	75,419	97,898
EXPENSES		
Publishing	61,570	35,108
Reprints	4,127	9,430
Circulation	7,653	7,942
Editing	2,652	3,628
Office Assistant	5,000	5,000
Honoraria	9,000	6,000
GST	5,146	3,867
Other	421	1,028
	95,569	72,003
EXCESS EXPENSES OVER REVENUE	$ (20,150)	$ 25,895

The Ottawa Field-Naturalists' Club Notes to the Financial Statements
September 30, 2002

1. CASH

	2002	2001
Chequing	$ 5,589	$ 3,358
Savings	58,336	36,984
Nesbitt Burns	919	4,265
Fletcher Wildlife Garden	5,868	6,153
	$ 70,712	$ 50,760

Investment Certificates:	Maturity Value	Maturity Date	Yield	Book Value
	$ 20,180	11/29/02	1.00%	$ 20,148
	21,644	12/30/02	1.00%	21,590
	43,303	04/30/03	1.00%	43,052
				$ 84,790

2. MARKETABLE SECURITIES

	Maturity Value	Maturity Date	Yield	Book Value
Ontario Savings Bonds	20,000	06/21/03	6.5%	$ 20,712
Province of Manitoba Coupon	29,847	11/15/04	5.119%	26,754
Ontario Savings Bonds	40,000	06/21/05	6.45%	41,370
CMHC Global Debs	$ 52,000	12/01/06	5.250%	53,539
Province of Ontario Bond	30,000	09/12/07	6.125%	31,187
Province of Newfoundland Bond	20,000	10/07/08	6.263%	20,538
Government of Canada Coupon	30,167	12/01/09	5.605%	20,590
Province of New Brunswick Bond	20,000	06/15/10	6.231%	21,068
				$235,758

3. CAPITAL ASSETS
Equipment at a cost of $16,748 is fully amortized.

4. FLETCHER WILDLIFE GARDEN

	2002	2001
REVENUE		
Federal government	$ 3,059	$ 3,055
City of Ottawa	1,450	–
Taverner Cup	1,354	1,307
Sales	872	–
GST	398	–
Donations	292	–
Other	–	3,955
	7,425	8,317
EXPENSES		
Program	3,174	3,220
Backyard	1,123	311
Habitats	1,864	51
Interpretation centre	783	226
Administration	1,048	1,119
Publications	337	–
GST	303	–
Library	87	22
Other	–	1,087
	8,719	6,036
	$ 1,294	$ 2,2815.

The Ottawa Field Naturalists' Club Statement Of Changes In Net Assets For the Year Ended September 30, 2002 (Note 5)

Net Assets	Beginning Balance	Excess Expenses CFN	Excess Expenses OFNC	Other Revenue	Expenses	Ending Balance
Unrestricted	$ 99,427	$ (20,150)	$ (2,621)	$ 3,669	$ –	$ 80,325
Club Reserve	100,000	–	–	–	–	100,000
Manning Principal	100,000	–	–	–	–	100,000
Manning – OFNC (a)	2,186	–	–	1,268	1,491	1,963
Manning – CFN (b)	8,225	–	–	5,074	120	13,179
Seedathon	1,569	–	–	1,086	568	2,087
Anne Hanes Memorial	870	–	–	–	–	870
de Kirilin-Lawrence (c)	24,553	–	–	478	1,056	23,975
Macoun Baillie Birdathon (d)	(7)	–	–	1,334	–	1,327
Alfred Bog (e)	615	–	–	51,659	–	52,274
	$ 337,438	$ (20,150)	$ (2,621)	$ 64,568	$ 3,235	$ 376,000

STATEMENT OF CHANGES IN NET ASSETS

a) Taverner Competition, $1,250; Peregrine Watch, $241;
b) CFN Vol. 115, No. 3, pp. 515-6, "Observation of a Golden Eagle attack on a Harlequin Duck", Heath, et al.;
c) Contribution toward purchase of Cameron Ranch on the Carden Plain alvar, $1,000;
d) Canadian Nature Federation, $1,035, Baillie Birdathon, $299;
e) As a result of the fund raising campaign begun in April 2002, in October 2002, $55,000 was sent to the Nature Conservancy of Canada.

The Ottawa Field Naturalists' Club Summary of Significant Accounting Policies

September 30, 2002

1. Nature of Business

The organization is non-profit and incorporated under the laws of Ontario (1884). The organization promotes the appreciation, preservation, and conservation of Canada's natural heritage. It encourages investigation and publishes the results of the research in all fields of natural history and diffuses information on these fields as widely as possible. It also supports and cooperates with other organizations engaging in preserving, maintaining or restoring environments of high quality for living things.

2. Financial Instruments

The organization's financial instruments consist of cash, accounts receivable, marketable securities, and accounts payable. Unless otherwise noted, it is the management's opinion that the organization is not exposed to significant interest, currency, or credit risks arising from these financial instruments. The fair value of these instruments approximate their carrying values.

3. Capital Assets

Capital assets acquired after 1989 are expensed. Capital assets acquired prior to 1990 were recorded as assets at cost and amortized on a straight-line basis. These assets have been fully amortized.

4. Statement of Changes in Financial Position

A statement of changes in financial position has not been provided as it would not provide additional meaningful information.

5. Foreign Currency

Transactions during the year in U.S. dollars have been converted in the accounts to Canadian dollars at the exchange rate effective at the date of the transaction. All monetary assets in U.S. dollars at year end have been converted to Canadian dollars at the rate effective on Sept. 30, 2002.

Gains or losses resulting therefrom are included in revenue or expenses.

Advice for Contributors to *The Canadian Field-Naturalist*

Content

The Canadian Field-Naturalist is a medium for the publication of scientific papers by amateur and professional naturalists or field-biologists reporting observations and results of investigations in any field of natural history provided that they are original, significant, and relevant to Canada. All readers and other potential contributors are invited to submit for consideration their manuscripts meeting these criteria. The journal also publishes natural history news and comment items if judged by the Editor to be of interest to readers and subscribers, and book reviews. Please correspond with the Book Review Editor concerning suitability of manuscripts for this section. For further information consult: A Publication Policy for the Ottawa Field-Naturalists' Club, 1983. *The Canadian Field-Naturalist* 97(2): 231-234. Potential contributors who are neither members of *The Ottawa Field-Naturalists' Club* nor subscribers to *The Canadian Field-Naturalist* are encouraged to support the journal by becoming either members or subscribers.

Manuscripts

Please submit, **to the Editor,** in either English or French, **three** complete manuscripts **written in the journal style.** The research reported should be original. It is recommended that authors ask qualified persons to appraise the paper before it is submitted. All authors should have read and approved it. Institutional or contract approval for the publication of the data must have been obtained by the authors. Also authors are expected to have complied with all pertinent legislation regarding the study, disturbance, or collection of animals, plants or minerals. The place where voucher specimens have been deposited, and their catalogue numbers, should be given. Latitude and longitude should be included for all individual localities where collections or observations have been made.

Print the manuscript on standard-size paper, **doublespace throughout,** leave generous margins to allow for copy marking, and **number each page.** For Articles and Notes provide a bibliographic strip, an abstract and a list of key words. Generally, words should not be abbreviated but use SI symbols for units of measure. The names of authors of scientific names should be omitted except in taxonomic manuscripts or other papers involving nomenclatural problems. "Standard" common names (with initial letters capitalized) should be used at least once for all species of higher animals and plants; all should also be identified by scientific name.

The names of journals in the Literature Cited should be written out in full. Unpublished reports and web documents should not be cited here but placed in the text or in a separate Documents Cited section. List the captions for figures numbered in arabic numerals and typed together on a separate page. Present the tables each titled, numbered consecutively in arabic numerals, and placed on a separate page. Mark in the margin of the text the places for the figures and tables.

Check recent issues (particularly Literature Cited) for journal format. Either "British" or "American" spellings are acceptable in English but should be consistent within one manuscript. **The Oxford English Dictionary, Webster's New International Dictionary** and le **Grand Larousse Encyclopédique** are the authorities for spelling.

Illustrations

Photographs should have a glossy finish and show sharp contrasts. Electronic versions should be high resolution. Photographic reproduction of line drawings, **no larger than a standard page,** are preferable to large originals. Prepare line drawings with India ink on good quality paper and letter (don't type) descriptive matter. Write author's name, title of paper, and figure number on the lower left corner or on the back of each illustration.

Reviewing Policy

Manuscripts submitted to *The Canadian Field-Naturalist* are normally sent for evaluation to an Associate Editor (who reviews it or asks another qualified person to do so), and at least one other reviewer, who is a specialist in the field, chosen by the Editor. Authors are encouraged to suggest names of suitable referees. Reviewers are asked to give a general appraisal of the manuscript followed by specific comments and constructive recommendations. Almost all manuscripts accepted for publication have undergone revision—sometimes extensive revision and reappraisal. **The Editor makes the final decision** on whether a manuscript is acceptable for publication, and in so doing aims to maintain the scientific quality, content, overall high standards and consistency of style, of the joumal.

Special Charges — Please take note

Authors **must share in the cost of publication** by paying $80 for each page, plus $15 for each illustration (any size up to a full page), and up to $80 per page for tables (depending on size). Authors may also be charged for their changes in proofs. Reproduction of color photos is extremely expensive; price quotations may be obtained from the Business Manager. If grant or institutional funds are not available, club members and subscribers may apply for a waiver of charges for the first five pages.

Limited joumal funds are available to help offset publication charges to authors with minimal financial resources. Requests for financial assistance should be made to the Business Manager when the manuscript is accepted.

Reprints

An order form for the purchase of repents will accompany the galley proofs sent to the authors.

FRANCIS R. COOK, Editor
RR 3 North Augusta, Ontario KOG IR0 Canada

Capture locations of Coyotes, *Canis latrans*, Bobcats, *Lynx rufus*, and Racoons, *Procyon lotor,* relative to home range boundries PHILIP S. GIPSON and JAN F. KAMLER 472

The Chain Dogfish, *Scyliorhinus retifer* (Garman, 1881), new to the Canadian Atlantic ichthyofauna JOHN GILHEN, BRIAN W. COAD, and ANDREW HEBDA 475

First record of Mink Frog, *Rana septentrionalis,* for insular Newfoundland IAN G. WARKENTIN, CHRISTINE E. CAMPBELL, KRISTIN G. POWELL, and TINA D. LEONARD 477

Northern Harrier, *Circus cyaneus,* attacks on Greater Sage-Grouse, *Centrocercus urophasianus,* in southern Alberta QUINN E. FLETCHER, CRAIG W. DOCKRILL, D. JOANNE SAHER, and CAMERON L. ALDRIDGE 479

Tributes

A tribute to Clarence Frankton 1906-2000 DANIEL F. BRUNTON 481

Book Reviews

ZOOLOGY: Ontario Odonata, Volume 3 — Mammals of Ontario — Mammals of North America — The Complete Guide to Antarctic Wildlife — Reptiles and Amphibians of Algonquin Provincial Park — Herpetology in Montana — Guide to the Reptiles of the Eastern Palearctic — Herpetology: An Introductory Biology of Amphibians and Reptiles, Second Editon — In Quest of Great Lakes Ice Age Vertebrates — Snakes of the United States and Canada 487

BOTANY: The Illustrated Encyclopedia of Trees — Carnivorous Plants of the United States and Canada: Second Edition — An Eclectic Guide to Trees East of the Rockies 496

ENVIRONMENT: Life, Temperature, and the Earth — City Wilds: Essays and Stories about Urban Nature — Conservation Biology — Ecological Basis for Stand Management: A Summary and Synthesis of Ecological Reponses to Wildfire and Harvesting in Boreal Forests — Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests — The Sacred Balance: A Visual Celebration of Our Place in Nature — Great Wildlife of the Great Plains — The Last Island: A Naturalist's Sojorn on Triangle Island — Nature by Design — Spreadsheet Exercises in Ecology and Evolution — Spreadsheet Exercises in Conservation Biology and Landscape Ecology — Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis 498

MISCELLANEOUS: A Bird in the Bush — Farley: The Life of Farley Mowat 508

NEW TITLES 511

News and Comment

Point Pelee Natural History News 3(2) — Canadian Species at Risk May 2003 — Marine Turtle Newsletter (101) — Froglog: Newsletter of the Declining Amphibian Populations Task Force (58) 513

Minutes of the 124th Annual Business Meeting of The Ottawa Field-Naturalists' Club Tuesday 14 January 2003 514

Advice to Contributors 522

Mailing date of the previous issue 117(2): 23 March 2004

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 01057 8771

THE CANADIAN FIELD Volume 117 Number 3 2003

Articles

Does removal of duck nest predators affect the temporal patterns of predation for simulated nests of grassland songbirds? NANCY DION, KEITH A. HOBSON, and SERGE LARIVIERE 347

Characteristics of early-winter Caribou, *Rangifer tarandus caribou*, feeding sites in the southern Purcell Mountains, British Columbia TREVOR A. KINLEY, JOHN BERGENSKE, JULIE-ANNE DAVIES, and DAVID QUINN 352

A review of the Canada Lynx, *Lynx canadensis*, in Canada KIM G. POOLE 360

Ecological aspects of a Wood Turtle, *Glyptemys insculpta*, population at northern limit of its range in Quebec ANDREW D. WALDE, J. ROGER BIDER, CLAUDE DAIGLE, DENIS MASSE, JEAN-CLAUDE BOURGEOIS, JACQUES JUTRAS, and ROGER D. TITMAN 377

Small mammal abundance and diversity in forests with and without Canada Yew, *Taxus canadensis* JERROLD L. BELANT and STEVE K. WINDELS 389

Lack of evidence for impact of the European White Birch, *Betula pendula*, on the hydrology of Wainfleet Bog, Ontario JOSUA DIAMOND, MARK BROWNING, ANDREW WILLIAMS, and JOHN MIDDLETON 393

Historical changes and current distribution of Caribou, *Rangifer tarandus*, in Quebec REHAUME COURTOIS, JEAN-PIERRE OUELLET, ANDRE GINGRAS, CLAUDE DUSSAULT, LAURIER BRETON, and JEAN MALTAIS 399

The Wood Turtle, *Glyptemys insculpta*, at River Denys: a second population for Cape Breton Island, Nova Scotia ANDREAS GRÄF, JOHN GILHEN, and JIL D. ADAMS 415

Limits to plasticity in Gray Wolf, *Canis lupus*, pack structure: conservation implications for recovering populations THOMAS M. GEHRING, BRUCE E. KOHN, JOELLE L. GEHRING, and ERIC M. AANDERSON 419

Den site activity patterns of adult male and female Swift Foxes, *Vulpes velox*, in northwestern Texas PATRICK R. LEMONS, WARREN B. BALLARD, ROBERT M. SULLIVAN, and MARSHA A. SOVADA 424

Energy cost of running in an Arctic Fox, *Alopex lagopus* EVA FUGLEI and NILS A. ORITSLAND 430

Population structure, growth, and age estimation of Spotted Turtles, *Clemmys guttata*, near their northern limit: an 18-year follow-up DAVID C. SEBURN 436

First record of the European Giant File Clam, *Acesta excavata* (Bivalvia: Pectinoidea: Limidae) in the Northwest Atlantic JEAN-MARC GAGNON and RICHARD L. HAEDRICH 440

Additions and range extensions to the vascular plant flora of the continental Northwest Territories and Nunavut, Canada, II WILLIAM J. CODY, KENNETH L. READING, and JENNIFER M. LIN

Notes

Black color morph of the Brown Lemming, *Lemmus trimucronatus* = *L. sibiricus* DENVER W. HOLT, MICHAEL T. MAPLES, and CHRIS SAVOK 466

White color phase of the Swift Fox, *Vulpes velox* JAN F. KAMLER and WARREN B. BALLARD 468

Death of Gray Wolves, *Canis lupus*, in Porcupine, *Erethizon dorsatum*, dens in Wisconsin ADRIAN P. WYDEVEN, SARAH R. BOLES, RONALD N. SCHULTZ, and THOMAS C. J. DOOLITTLE 469

ISSN 0008-3550

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 01226 6193

QH
1
C213
NH

The CANADIAN FIELD-NATURALIST

Published by THE OTTAWA FIELD-NATURALISTS' CLUB, Ottawa, Canada

Volume 117, Number 4

October–December 2003

The Ottawa Field-Naturalists' Club

FOUNDED IN 1879

Patrons

Her Excellency The Right Honourable Adrienne Clarkson, C.C., C.M.M., C.D.
Governor General of Canada
His Excellency John Ralston Saul, C.C.

The objectives of this Club shall be to promote the appreciation, preservation and conservation of Canada's natural heritage; to encourage investigation and publish the results of research in all fields of natural history and to diffuse information on these fields as widely as possible; to support and cooperate with organizations engaged in preserving, maintaining or restoring environments of high quality for living things.

Honorary Members

Edward L. Bousfield	Bruce Di Labio	John A. Livingston	E. Franklin Pope
Donald M. Britton	R. Yorke Edwards	Stewart D. MacDonald	William O. Pruitt,, Jr.
Irwin M. Brodo	Anthony J. Erskine	Hue N. MacKenzie	Joyce and Allan Reddoch
William J. Cody	John M. Gillett	Theodore Mosquin	Mary E. Stuart
Francis R. Cook	C. Stuart Houston	Eugene G. Munroe	John B. Theberge
Ellaine Dickson	George F. Ledingham	Robert W. Nero	Sheila Thomson

2003 Council

President: Gary McNulty	Ronald E. Bedford	Francis R. Cook	Cendrine Huemer
Vice-President: Mike Murphy	John Cameron	Barbara Gaertner	John Roy
Gillian Marston	Janet Castle	Marcel Gahbauer	Stanley Rosenbaum
Recording Secretary: Ken Alhson	Charlie Clifford	Diane Lepage	Louise Schwartz
Treasurer: Frank Pope	William J. Cody	Karen McLachalan Hamilton	David Smythe
Past President: Eleanor Zurbrigg	Kathy Conlan	David Hobden	Chris Traynor

To communicate with the Club, address postal correspondence to: The Ottawa Field-Naturalists' Club, P.O. Box 35069, Westgate P.O. Ottawa, Canada K1Z 1A2, or e-mail: ofnc@achilles.net.
For information on Club activities telephone (613) 722-3050 or check http//www.achilles.net/ofnc/index.htm

The Canadian Field-Naturalist

The *Canadian Field-Naturalist* is published quarterly by The Ottawa Field-Naturalists' Club. Opinions and ideas expressed in this journal do not necessarily reflect those of The Ottawa Field-Naturalists' Club or any other agency.

We acknowledge the financial support of the Government of Canada toward our mailing cost through the Publication Assistance Program (PAP), Heritage number 09477.

Editor: Dr. Francis R. Cook, R.R. 3, North Augusta, Ontario KOG IR0; (613) 269-3211; e-mail: fcook@achilles.net
Copy Editor: Elizabeth Morton
Business Manager: William J. Cody, P.O. Box 35069, Westgate P.O. Ottawa, Canada KIZ 1A2; (613) 759-1374
Book Review Editor: Roy John, 2175 Emard Crescent, Ottawa, Ontario K1J 6K5; e-mail: roy.john@pwgsc.gc.ca

Associate Editors:	Robert R. Anderson	Paul M. Catling	David Nagorsen
	Charles D. Bird	Brian W. Coad	Donald F. McAlpine
	Robert R. Campbell	Anthony J. Erskine	William O. Pruitt, Jr.

Chairman, Publications Committee: Ronald E. Bedford

All manuscripts intended for publication except Book Reviews should be addressed to the Editor and sent by postal mail. Book-review correspondence should be sent by e-mail or postal mail to Roy John, Book-review Editor.

Subscriptions and Membership
Subscription rates for individuals are $28 per calendar year. Libraries and other institutions may subscribe at the rate of $45 per year (volume). The Ottawa Field-Naturalists' Club annual membership fee of $28 (individual) $30 (family) $50 (sustaining) and $500 (life) includes a subscription to *The Canadian Field-Naturalist*. All foreign subscribers and members (including USA) must add an additional $5.00 to cover postage. The club regional journal, *Trail & Landscape*, covers the Ottawa District and Local Club events. It is mailed to Ottawa area members, and available to those outside Ottawa on request. It is available to Libraries at $28 per year. Subscriptions, applications for membership, notices of changes of address, and undeliverable copies should be mailed to: The Ottawa Field-Naturalists Club, P.O. Box 35069, Westgate P.O. Ottawa, Canada K1Z 1A2. Canada Post Publications Mail Agreement number 40012317. Return Postage Guaranteed. Date of this issue: October–December 2003.

COVER: Juvenile Pink Salmon, *Oncorhynchus gorbuscha,* infested with the Sea Louse, *Lepeophtheirus salmonis*, Burdwood Islands, British Columbia, 23 June 2001, photo by Alexandra Morton. See pages 634-641.

SMITHSONIAN
OCT 12 2004
LIBRARIES

The Canadian Field-Naturalist

Volume 117, Number 4 September–December 2003

Canopy Interception of Acid Deposition in Southern Ontario

Jules Carlson[1], William A. Gough[1], Jim D. Karagatzides[2], and Leonard J. S. Tsuji[1]

[1]Department of Physical and Environmental Sciences, University of Toronto at Scarborough, 1265 Military Trail, Scarborough, Ontario M1C 1A4 Canada
[2]Department of Geography, Queen's University, Kingston, Ontario K7L 3N6 Canada
[3]Department of Environment and Resource Studies, University of Waterloo, Waterloo, Ontario N2L 3G1 Canada

Carlson, Jules, William A. Gough, Jim D. Karagatzides, and Leonard J. S. Tsuji. 2003. Canopy interception of acid deposition in southern Ontario. Canadian Field-Naturalist 117(4): 523-530.

The impact of tree canopies on acid deposition was examined. Differences in the chemical composition of unintercepted precipitation (dustfall) and canopy was intercepted precipitation (throughfall) at 18 southern Ontario forests, collected during the summers of 1995-1996, were chemically analyzed. The methodology of collection and analysis validated using consistency checks for interception loss, maintenance of electrical neutrality and ion correlation. T-test analyses found throughfall fluxes of K^+, Ca^{2+}, Mg^{2+}, and NO_3^- were significantly higher than dustfall flux ($p < 0.05$), consistent with other studies. Barrie and nearby sites at Orillia and Bracebridge had larger dustfall depositions of base cations and Cl^- suggesting a nearby source of these ions. T-tests revealed large exceedances of pH and sulphate concentration in dustfall over throughfall at the two Scarborough sites; a local point source of sulphates in the Greater Toronto Area was suspected.

Key Words: acid deposition, canopy interception, dustfall, throughfall, Ontario.

Acid rain emerged as an environmental issue after the Industrial Revolution beginning in the 1820s. The term "acid rain" was first used in the 1850s (Howells 1990). More formally the term, acid deposition, today represents material deposited from the atmosphere onto the Earth's surface, with a pH lower than 5.6 (Foster 1993). The main precursors to acid deposition are emissions of sulphur and nitrogen dioxides, as well as chlorinated compounds. These precursors form sulphuric acid, nitric acid and hydrochloric acid. Although natural sources of these precursors exist, the majority are emitted from anthropogenic sources such as smelters, utilities, and vehicles.

Acid deposition, especially in the form of acid rain, has had detrimental effects on aquatic, terrestrial and man-made structures (Ministry of the Environment 1986; Environment Canada 1991). In particular, acid rain can have a deleterious effect on our ecosystems impacting the forest canopy and soils. Poorly buffered soils are robbed of their nutrients leading to poor forest health and the commonly observed crown dieback. In highly acidic conditions, aluminium is leached from soils in a cation exchange. This can have devastating effects on local aquatic populations. Although emission control strategies have reduced precursor emissions of sulphates, these reductions have not been sufficient to mitigate this problem and acid rain monitoring needs to continue (Kumar et al. 2001).

Of particular interest is the impact of acid rain on forest canopies. The chemical composition and volume of incident precipitation change when it passes through a forest canopy. Interception loss of precipitation has been reported in the range of 6 – 43% for deciduous forests (Helvey and Patric 1965). Differences in the chemical composition of dustfall (unintercepted precipitation) and throughfall (forest canopy intercepted precipitation) can be attributed to both wet and dry deposition and the uptake or release of compounds by the leaves (Balestrini et al. 1998; Houle et al. 1999).

Ion exchanges can produce a net change in the concentrations of positive and negative ions dissolved in throughfall. Normally there is a net increase in ion concentration in throughfall (Gaber and Hutchinson 1988a, 1988b; Gjengedal 1996; Prakasa Rao et al. 1995; Houle et al. 1999). The size of positive charge from the net change in cation concentration must equal the size of negative charge from the net change in anion concentration.

Most studies have found enrichment of K^+, Ca^{2+}, Mg^{2+}, Na^+, SO_4^{2-}, NO_3^- and Cl^- in throughfall while H^+ and NH_4^+concentrations are usually reduced (Gaber and Hutchinson 1988b; Gjengedal 1996; Prakasa Rao et al. 1995; Houle et al. 1999). As much as 90% of the H^+ in precipitation passing through a canopy can be absorbed by the leaves (Cappellato et al. 1993). Release of ions from leaves, referred to as foliar leach-

ing, has been observed for K^+, Ca^{2+}, Mg^{2+}, and other base cations (Lindberg et al. 1985; Houle et al. 1999). Foliar leaching is usually minimal for SO_4^{2-}, Cl^-, and Na^+ (Granat and Hallgren 1992; Cape et al. 1992; Veltkamp and Wyers 1997). NO_3^- can be either absorbed or leached (Neary and Gizyn 1994). Mechanisms for foliar leaching include passive cation exchange for H^+ with the cuticle cell wall (Mecklenberg et al. 1966), the cell interior (Eaton et al. 1973), or the other cells in the interior of the leaf (Burkhardt and Drechsel 1997).

The ecological health implications of acid deposition have prompted much research and monitoring activity, but a recent lack of government funding has slowed both monitoring and research efforts. For two summers, Monitoring Acid Rain Youth Program (MARYP) monitored acid rain and its impacts on local environments in south-central Ontario (Figure 1). The monitoring program included the collection of dustfall and throughfall precipitation and its subsequent chemical analysis. It also included surveys of local tree species, bird populations, frogs, and wildflowers in an ecosystem approach. High school students were hired to collect the precipitation during the months of July and August and to conduct the ecological surveys. Kumar et al. (2001) found the resulting acid rain data to be of high quality when used in a critical load assessment (Arp et al. 1996). Gough et al. (2002) examined the suitability of using a summer-only monitoring program by examining acid rain data collected by Environment Canada in the same region.

In this paper, we expand on the earlier analyses by comparing dustfall and throughfall rain chemistry in south-central Ontario, Canada, during the summers of 1995 and 1996, collected in the Monitoring Acid Rain Youth Program (MARYP). Although others have assessed the validity of the precipitation and soil chemistry data collected in this program (Kumar et al. 2001), we include three additional tests of data robustness and consistency for samples collected. In addition, we explore the impact of the forest canopy on rainfall chemistry. Finally, differences in ion fluxes and pH of dustfall and throughfall between urban and rural sites are examined.

Methods

Data Collection

The pH and chemical composition of acid deposition collected in 18 forests of south-central Ontario (Figure 1) were determined (rainwater samples, throughfall and dustfall) as part of the Monitoring Acid Rain Youth Program (MARYP; Karagatzides et al. 1997*). The samples were collected during the months of July and August (1995 and 1996) at five locations, with two forests at each location. The Peterborough forests were sampled both years. Sample sites had a variety of forest cover: predominantly sugar maple; mixed deciduous; and mixed coniferous. At each forest site, four dustfall collectors and four throughfall collectors were installed and sampled weekly. The volume in each collector was recorded using a graduated container and pH measured using a portable pH kit. Composite dustfall and throughfall samples were produced, by pooling samples from the four throughfall and the four dustfall collection locations, for each forest. The result was that only one dustfall and one throughfall sample was chemically analyzed for each collection. The acidifying compounds (SO_4^{2-}, NO_3^-, Cl^-, F^-, and PO_4^{2-}) were analyzed by ion chromatography (Dionex 2010i), and base cations (K^+, Ca^{2+}, Na^+, Mg^{2+}, and Fe^{2+}) were measured by ICP-mass spectrometry (Perkin-Elmer ELAN 5000).

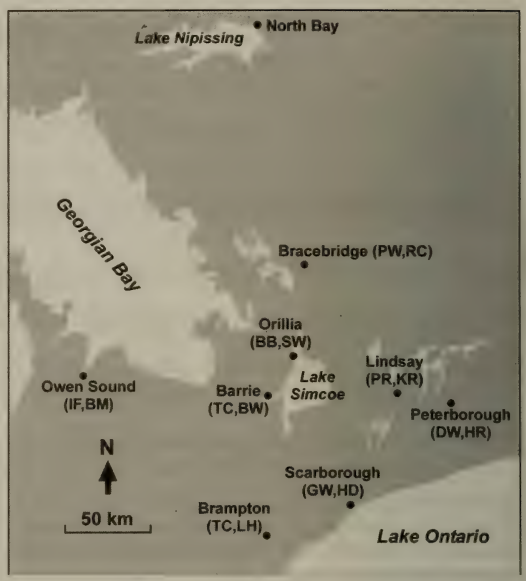


FIGURE 1. Map of MARYP sites in southern Ontario.

Samples were filtered through Whatman #42 immediately and frozen. Samples for ICP-MS were acidified with nitric acid to a final concentration of 2% HNO_3. Analytical instruments were calibrated with NIST stock standards and the calibration curve checked with a different reference standard. Blind pH buffers of known concentrations were sent to all field assistants and results were always within +/- 0.1 pH units.

Dustfall and throughfall fluxes, determined from elemental concentration and rainfall volume, were extrapolated to a per hectare basis and the total flux determined as the difference between dustfall and throughfall. The weekly fluxes were summed over the sampling period. Dustfall and throughfall samples from North Bay were mistakenly pooled into one composite sample containing rainwater from both dustfall and throughfall collection, so chemical analysis was not performed, only pH values were included in the

* See Documents Cited section.

data analysis.

Ion fluxes and pH of dustfall and throughfall were compared using paired, two sided t-tests. Statistical relationships among cations were explored by correlating base cation net concentrations (dustfall concentration – throughfall concentration) with H^+ and anion net concentrations. The net change in total anion charge and total cation charge were calculated by summing the net change in the concentration of each anion or cation weighted by the magnitude of its charge. The net changes in total anion charge and in total cation charge was compared. The magnitude of net ion fluxes were compared between Scarborough forests and the average of the 16 other sites to determine differences between urban and rural areas. Although Brampton could be construed to be an urban site, the Scarborough sites were directly downwind of the Greater Toronto Area. Differences were deemed significant if ion fluxes from Scarborough sites were outside the 99% confidence interval described by the other sites.

Data Analysis

CONSISTENCY CHECKS: Three separate internal consistency checks were performed. To determine whether the sample volumes collected were within the range of previous work, calculated interception losses for the canopies studied were compared to interception losses found in other studies. The other two checks, charge balance and ion correlation, were performed to determine whether the measured concentrations of ions in the dustfall and throughfall collectors were internally consistent. Differences between net rainfall concentration of H^+, K^+, Ca^+, Mg^{2+}, Na^+, SO_4^{2-}, NO_3^-, and Cl^- (ion concentrations of dustfall minus ion concentrations of throughfall) were correlated (Pearson multiple correlation).

Within each study site, pH differences for throughfall and dustfall were assessed using t-tests. Finally urban and rural differences were analyzed. Statistica was used for all statistical analyses.

Results and Discussion

Consistency Checks

RAINFALL INTERCEPTION: The average values for canopy interception loss of 14 +/- 9% and 15 +/- 9% (Tables 1 and 2) for 1995 and 1996, respectively, fall within the range (between 11 and 22%) of interception loss values from other studies performed in deciduous or mixed temperate forests of North America or Europe (Helvey and Patric 1965; Robson et al. 1994; Gash et al. 1995; Carlyle-Moses and Price 1999).

The Limehouse site in Brampton was not considered in the interception loss average since the measured rainfall volume in throughfall collectors exceeded the measured rainfall volume in dustfall collectors. The larger dustfall rainfall volume is either the result of spatial inhomogenity of precipitation or measurement or analysis error. At this site the dustfall collectors were over 100 m away from the throughfall collectors, the largest separation in the study.

CHARGE BALANCE: Exchanges between rainfall and leaf surfaces can change the concentrations of positive and negative ions dissolved in throughfall precipitation. However, the associated charges of these ions must balance since the rainwater must remain neutral throughout the ion exchange processes. All sites except Tiffin Conservation (TC, Barrie) showed a net loss of both cations and anions from the canopy into the throughfall precipitation (Table 3). The gain of both anion and cation charge at this station is anomalous being suggestive of field sample contamination. Therefore, the average change in charge is calculated without the TC data. The net change in anion charge was 74% greater when the Barrie site was not considered. This suggests that the ions not measured in the analysis (mostly organic ions) were predominantly negatively charged. Lovett et al. (1985) found that organic anions had a significant effect on maintaining the charge balance and in countering cation leaching.

TABLE 1. Total rainfall volumes collected in both dustfall (DF) and throughfall (TF) gauges from all sites of the 1995 MARYP study. The percentage reductions in throughfall volumes due to interception are given for each forest.

Location	DW	HR	PR	KR	PW	RC	IF	BM	TR	LH	
DF (L)	2.6	1.9	1.9	1.4	2.6	3.2	2.3	2	2.5	1.7	
TF (L)	2.1	1.8	1.6	1.3	2.2	2.9	1.5	1.9	2.1	2.2	Average (9)
% Interception	19	5	16	7	15	9	35	5	16	-29	14+/- 9

TABLE 2. Total rainfall volumes collected in both dustfall and throughfall gauges from all sites of the 1996 MARYP study. The percentage reductions in throughfall volumes due to interception are given for each forest. Data are not available for the North Bay forests.

Location	DW	HR	GW	HD	TC	BW	BB	SW	
DF (L)	1.1	1.7	2.1	1.5	1.5	3.5	2.5	2.6	
TF (L)	0.8	1.5	1.8	1.1	1.4	2.9	2.5	2.1	Average (8)
% Interception	27	12	14	27	6.7	17	0.0	19	15 +/- 9

To investigate if the observed difference in net charge can be explained by ions that were not measured, a correlation (Pearson) was performed between the changes in total positive and negative internal charge, between dustfall and throughfall. The net change in total anion charge and total cation charge revealed a strong significant correlation ($r^2 = 0.73$, $p < 0.001$; Table 3).

ION CORRELATION CONSISTENCY CHECK: Significant correlations were observed between the net concentration of SO_4^{2-} and of the base cations, K^+ and Ca^{2+}. Correlations between NO_3^- and K^+ and Ca^{2+} and Mg^{2+} were also found to be statistically significant ($p < 0.05$) (Table 4). These results are consistent with Skeffington and Sutherland (1995) and Jiang and Jagels (1999). Significant correlations were also observed between Mg^{2+} with K^+, Ca^{2+} and Na^+ (Table 4). However, H^+ net concentrations did not produce statistically significant correlations with K^+, Ca^{2+}, or Mg^{2+}. Some studies have reported strong correlations between net H^+ concentrations and net base cation concentrations (Gaber and Hutchinson 1988b; Liechty et al. 1993), while others have found no relationship (Hutchinson et al. 1986).

SO_4^{2-} net fluxes were also strongly correlated with NO_3^- net fluxes ($r^2 = 0.404$, $p < 0.01$). The strong correlation observed here may be attributed to a plume of pollutants from the southwest (Gough et al. 2002). Na^+ and Cl^- showed a significant correlation which may indicate that road salts from nearby urban areas or roadways are deposited as dry deposition.

SOURCE OF SALT NEAR BARRIE?: The two Barrie sites had significantly larger (more positive) net ion fluxes than the average for Cl^-, Na^+, Mg^{2+}, and Ca^{2+} as the net ion fluxes for the Barrie sites are outside of the 99% confidence intervals described by the other sites (Table 5). Therefore, significantly more of these ions were retained within the canopies of the two Barrie sites. Does this result from forests retaining more ions or is there more of the ions to begin with prior to reaching the canopy? For Cl^-, Na^+ and Mg^{2+} the dustfall values were the largest for the study region thus lending support to the second suggestion. Also higher than average concentrations of these ions were found in nearby Orillia and Bracebridge sites suggesting that there may be a source of base cations and Cl^- in this area (Table 5).

TABLE 3. The net change (DF-TF) in anion and cation concentrations for all 18 1995-1996 MARYP forests and with the Tiffin Conservation (TC) forest removed. Data for North Bay are not available.

	Mean (18 sites)	Mean (TC removed)
Cations	-0.175	-0.188
Anions	-0.094	-0.108
r^2	0.726	0.681
p-value	0.000	0.000

Chemical analysis of precipitation

Both base cations (K^+, Ca^{2+}, Mg^{2+}) and acid contributing anions (SO_4^{2-}, NO_3^-, Cl^-) were found to have greater throughfall depositions than dustfall depositions resulting in negative fluxes, while the opposite was observed for H^+. Rainfall was neutralized at all sites studied as a result of interaction with the forest canopy consistent with other studies of deciduous species dominated canopies.

PH MEASUREMENTS: The pH of the collected throughfall was significantly higher than the pH of the collected dustfall (t-test, $p < 0.05$) for both the 1995 and 1996 data (Figure 2), consistent with other studies (Lindberg et al. 1986; Gaber and Hutchinson 1988a; Liechty et al. 1993; Neary and Gizyn 1994; Prakasa Rao et al. 1995; Houle et al. 1999). The Scarborough sites showed a dustfall H^+ /throughfall H^+ ratio of approximately 25 and 50 (96 and 98% neutralization)

TABLE 4. Coefficients of determination (r^2) and their corresponding p-values are given for net concentrations of ions for 18 forest locations of the MARYP study from a Pearson multiple correlation. Significant p-values are denoted: *for $p < 0.05$, **for $p < 0.01$, ***for $p < 0.001$.

		H	K	Ca	Mg	Na	SO_4	NO_3	Cl
H	r^2	–	0.054	0.027	0.000	0.223	0.089	0.117	0.017
K	r^2		–	0.207	0.387*	0.000	0.252*	0.317*	0.136
Ca	r^2			–	0.403**	0.007	0.693***	0.573**	0.066
Mg	r^2				–	0.120	0.235	0.277*	0.204
Na	r^2					–	0.006	0.007	0.372
SO_4	r^2						–	0.404**	0.082
NO_3	r^2							–	0.896**
Cl	r^2								–

TABLE 5. Difference in net ion fluxes (in kg/ha) of Cl^-, Na^+, Mg^{2+}, and Ca^{2+} between the two Barrie forests and the average of the other 16 MARYP forests. The average net ion flux for the other 16 forests and the 99% confidence intervals (CI) of this dataset are also given.

Ion	Tiffin Conservation (TC)	Brigley's Woods (BW)	Average	99% CI of 16 Sites	
Cl^-	4.10	4.90	-0.75	-1.43	-0.66
Na^+	0.50	1.20	-0.20	-0.43	0.28
Mg^{2+}	0.60	0.70	-0.32	-0.56	-0.07
Ca^{2+}	-0.40	-0.30	-1.33	-2.24	-0.43

for the two sites, while Barrie and Orillia showed H^+ ratios of about 2 (50% neutralization) (Table 7).

The highest throughfall pH values were observed in Brampton (LH) in 1995 (6.8) and at the two Scarborough sites in 1996 (6.3 and 5.8), while the lowest pH throughfall values were observed in North Bay (4.5), Lindsay (KR) and at the two Bracebridge sites (Figure 2). There appears to be a reduction in the pH of throughfall precipitation with increasing latitude. The largest dustfall-throughfall differences in pH were observed at the two Scarborough sites (Figure 2) and may be attributed to increased deposition of SO_4^{2-} and NO_3^- (Figures 3 and 4).

CHEMICAL COMPOSITION OF IONS IN DUSTFALL VS. THROUGHFALL: Ion fluxes (dustfall – throughfall) were negative for K^+, Ca^{2+}, Mg^{2+}, Fe^{3+}, NO_3^-, SO_4^{2-} and Cl^-, positive for H^+, and similar for Na^+ (Table 6). Any percentages over 100 indicate a negative ion flux (i.e. throughfall greater than dustfall). Significant differences (t-test $p < 0.05$) were observed in both 1995 and 1996 for K^+, Ca^{2+}, and NO_3^-, while significant differences were only observed in 1995 for Mg^{2+} and in 1996 for SO_4^{2-} (Table 6).

ACID CONTRIBUTING ANIONS: Nitrate fluxes were significantly greater in throughfall than in dustfall for 1995 and 1996 (Table 6), consistent with most studies which have found negative net NO_3^- fluxes (Prakasa Rao et al., 1995; Houle et al., 1999). Dry deposition was reported to be the largest contributor to NO_3^- deposition (Lindberg et al., 1986) compared to foliar leaching, which usually makes a minimal contribution to the negative net NO_3^- fluxes (Puckett 1990; Potter 1991; Liechty et al. 1993; Houle et al. 1999). Results for SO_4^{2-} and Cl- were inconclusive. Significant negative SO_4^{2-} fluxes were observed for 1996; however, 1995 had a positive flux. The negative SO_4^{2-} fluxes are likely due to dry deposition onto leaf surfaces. Contributions to net sulphur concentration of throughfall from foliar leaching have been recorded to be as low as 3% (Cape et al. 1992; Granat and Hallgren 1992; Veltkamp and Wyers 1997). Cl^- showed significant negative net fluxes (Table 6) in 1995 but not in 1996. This may be related to the choice of locations which, differed from 1995 to 1996.

CATION ANALYSIS: The largest negative net cation flux was observed for K^+. The large difference in K^+ may be attributed to foliar leaching. Foliar leaching has been found to comprise nearly 70% of the net ion flux for K^+ (Cappellato et al. 1993) but there was no significant correlation between H^+ and K^+ in the MARYP

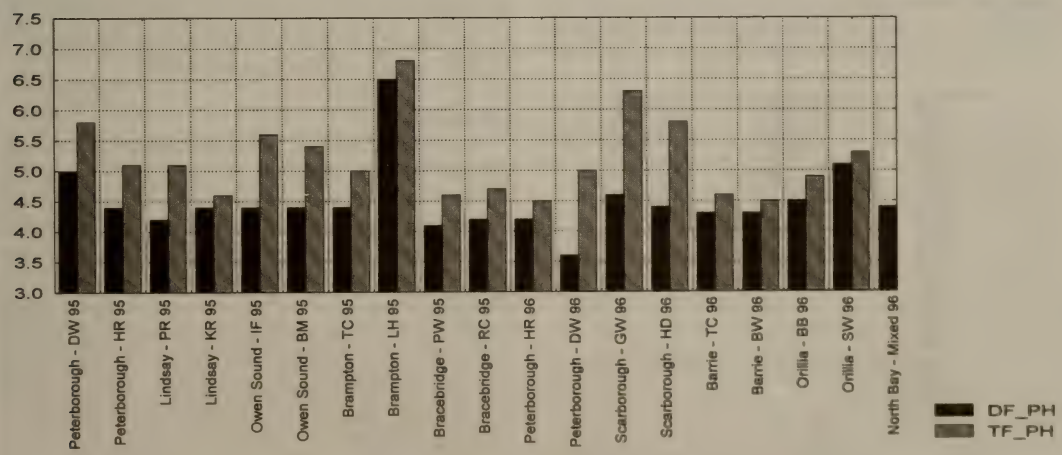


FIGURE 2. Comparison of pH between rainfall collected in throughfall and dustfall collectors in the 20 Ontario forests of the 1995-1996 MARYP study. The two letter acronyms below the pH columns represent individual MARYP sites.

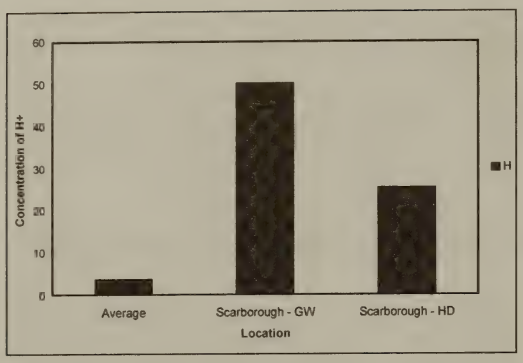


FIGURE 3. Ratio of dustfall to throughfall H^+ ion fluxes for the average of 16 MARYP forests compared to the dustfall to throughfall H^+ ratio for the two Scarborough forests. GW and HD represent the Scarborough forests Greenwood and Heber Down.

data ($p > 0.05$) (Table 4). Studies to determine relationships between H^+ deposition and K^+ leaching have given inconclusive results.

Both years showed significant differences between Ca^{2+} dustfall and throughfall deposition ($p < 0.05$) (Table 6). Canopy leaching makes a significant contribution (up to 60%) to the negative net canopy flux (Houle et al. 1999). Canopy leaching is believed to take place mainly by cation exchange (Mecklenberg et al. 1966; Gaber and Hutchinson 1988b; Gjengedal 1996).

The average Mg^{2+} flux was significantly greater in throughfall than in dustfall in 1995 ($p < 0.05$) (Table 6). Mg^{2+} fluxes are commonly larger in throughfall than in dustfall (Lindberg et al. 1986; Gaber and Hutchinson 1988b; Liechty et al. 1993; Neary and Gizyn 1994; Prakasa Rao et al. 1995; Houle et al. 1999).

Urban vs. Rural

The difference in chemical composition between throughfall and dustfall is strongly affected by dry deposition. To determine the location of sources of deposition, we examined the net ion deposition fluxes in sites near urban centres and in rural areas. Deposition of ions (particularly the acid contributing anions) is likely to be greater in urban areas resulting in larger ion fluxes if local point sources exist.

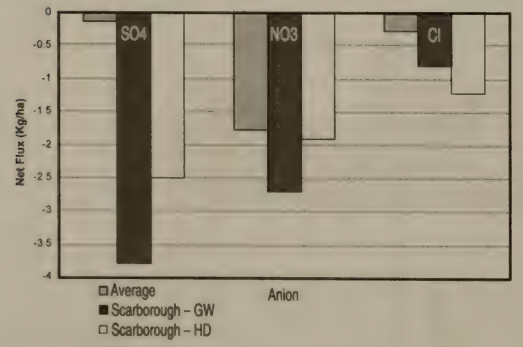


FIGURE 4. Net anion fluxes for the average of 16 MARYP forests compared to net anion fluxes for the two Scarborough forests. GW and HD represent the Scarborough forests Greenwood and Heber Down.

Net sulphate flux at the two Scarborough forests was more than 17 and 26 times as great as the average sulphate flux of the other forests in the study. Sulphate fluxes in Scarborough were outside the 99.9% confidence limits described by the other 16 sites indicating the likelihood of a point source for sulphates in the Greater Toronto Area. One possible source of sulphates is the large SO_2 emissions from the coal burning at the Lakeview Electrical Plant in Mississauga. Net fluxes of NO_3^- were also larger than average for the Scarborough sites but NO_3^- fluxes remained within the 99% confidence interval described by the other 16 forests. This is in agreement with Gough et al. (2002) who also found independent evidence of a sulfate source in the Greater Toronto Area using acid deposition data.

Scarborough forests had a much stronger buffering capacity than the more rural sites. The two Scarborough forests had dustfall/throughfall H^+ deposition ratios of 25 and 50, while the average dustfall/throughfall H^+ deposition ratio for all forests was only 6 (Table 7). This may be explained by the significantly larger dry deposition of sulphates at the Scarborough forests. (We assume that due to the close proximity of the dustfall and throughfall forests that the wet deposition for the two are identical). Larger sulphate dry depositions may result in greater ion exchange on leaf surfaces to neutralize the sulphuric and sulphurous acids formed when the sulphates dissolve in water on the leaf surface. Net fluxes of K^+ and Ca^{2+} were significantly higher (outside the 99% confidence limits) at the Scarborough forests than the average for the other forests (Table 7). Increased exchange would likely increase the uptake of H^+. Increased uptake of H^+ by the canopy results in increased neutralization of dustfall as it passes through the canopy.

Conclusions

In this work we have examined thoughfall and dustfall precipitation chemistry from 18 forests in south-central Ontario collected in the MARYP program during the summers of 1995 and 1996. Three internal consistency checks were performed on the data. For the most part the data were internally consistent. One anomaly arose when examining rainfall interception which had more throughfall rain volume than dustfall unlike all other locations and contrary to past observations. All other locations fell within published interception loss. This anomaly is likely due to either rainfall heterogeneity or possible sampling errors.

All sites with the exception of one of the Barrie sites showed a net loss of cation and anion charge from the canopy to the throughfall precipitation consistent with the scientific literature. The changes in anion

TABLE 6. Comparison of dustfall and throughfall deposition fluxes for eight major ions for 10 forests in 1995 (9 degrees of freedom) and for eight forest sites in 1996 (7 degrees of freedom). The comparisons are also given for pooled 1995 and 1996 data. P-values from two-sided dependent t-tests are given and the ratio of throughfall / dustfall is given as a percentage. $P < 0.05$ is designated with a *, $p < 0.001$ is designated with ***. All ions with a throughfall/dustfall percentage ratio above 100% are enriched in throughfall with respect to dustfall and have a negative net ion flux, and vice versa.

Year	1995 (9df)		1996 (7df)		Average (17 df)	
Ion	p-value	TF = % DF	p-value	TF = % DF	p-value	TF = % DF
K^+	0.000039 ***	478%	0.021 *	206%	0.000 ***	287%
Ca^{2+}	0.00060 ***	162%	0.025 *	154%	0.004 **	158%
Mg^{2+}	0.018 *	249%	0.63	124%	0.060	170%
Na^+	0.18	121%	0.95	99%	0.460	106%
Fe^{3+}	0.011 *	393%	0.027 *	135%	0.007 **	191%
SO_4^{2-}	0.50	93%	0.020 *	116%	0.754	103%
NO_3^-	0.020 *	194%	0.011 *	136%	0.000 ***	159%
Cl^-	0.028 *	148%	0.76	94%	0.710	106%

TABLE 7. Net ion fluxes of the average of 16 MARYP sites and the two most urban forests (Scarborough – Greenwood and Heber Downs). Ions with significantly different net fluxes at the Scarborough forests than from the average of the other forests are starred. H^+ is given as a ratio of concentrations of dustfall and throughfall in moles per litre. The other ion fluxes are given as differences between dustfall and throughfall in kg/ha.

Ion	Average	99% Conf. Int.		Scarborough – GW	Scarborough – HD
H^+	9.39	0.74	18.0	50 *	25 *
K^+	-2.17	-2.66	-1.09	-5.9 *	-3.1 *
Ca^{2+}	-1.23	-1.38	-0.40	-4.8 *	-3 *
Mg^{2+}	-0.211	-0.44	0.16	-1 *	-0.6 *
Na^+	-0.083	-0.43	0.29	-0.2	-0.2
Fe^{3+}	-9.77	-3.07	-15.1	-15	-14
SO_4^{2-}	-0.137	-0.89	1.37	-3.8 *	-2.5 *
NO_3^-	-1.78	-2.67	-0.75	-2.7 *	-1.9
Cl^-	-0.261	-1.55	1.42	-0.8	-1.2

and cation charge were strongly and significantly correlated as expected. However they were not balanced suggesting the presence of negatively charged organic anions which were not measured in this work.

The ion correlations linked sulphate with the base cations K^+ and Ca^{2+}, suggesting greater cation exchange in more acidic environments. Similarly nitrate was significantly correlated to K^+, Ca^{2+}, and Mg^{2+} . Sulphate and nitrate were significant correlated suggesting the pollutants were part of a plume passing through southern Ontario likely from the southwest consistent with Gough et al. (2002). Na^+ and Cl^- were strongly correlated suggesting road salts were deposited on the forest canopies as dry deposition.

The forest canopy acts as a chemical buffer reducing the pH of the throughfall precipitation. This can arise due to dry deposition on the leaves or through foliar leaching (cation exchange). Throughfall fluxes significantly exceeded dustfall fluxes for K^+, Ca^{2+}, Fe^{2+}, and NO_3^-, while dustfall fluxes are greater than throughfall fluxes for H^+, consistent with other studies. Much larger fluxes of base cations and Cl^- were observed for forests in Barrie, and nearby Orillia and Bracebridge sites, suggesting a source of base cations and Cl^- in this area.

Urban (Scarborough) forests had larger net sulphate fluxes and larger throughfall to dustfall H^+ ratios than the remaining rural forests. This may be explained by larger dry deposition of sulphates and may indicate a point source of sulphates in the GTA consistent with Gough et al. (2002). Further studies making comparisons of net depositions of ions between urban and rural areas are needed to further explore this issue.

Documents Cited (marked * in text)

Karagatzides, J. D., K. A. Bolton, S. Chow, R. R. Fulthorpe, W. A. Gough, D. Kozlovic, and **L. J. S. Tsuji**. 1997. Monitoring Acid Rain Youth Program Report #4: 1996 Final Report. (Peterborough, Ontario: Trent University).

Literature Cited

Arp, P. A., T. Oja, and **M. March.** 1996. Calculating critical S and N loads and current exceedances for upland forests in southern Ontario, Canada. Canadian Journal of Forest Research 26: 696-709.

Balestrini, R., L. Galli., A. Tagliaferri, and **G.Tartari**. 1998. Study on throughfall deposition in two north Italian forest sites (Vatellina, Lombardy). Chemosphere 36: 1095-1100.

Burkhardt, J., and **P. Drechsel**. 1997. The synergism between SO_2 oxidation and manganese leaching on spruce needles – a chamber experiment. Environmental Pollution 95: 1-11.

Cape, J. N., L. J. Sheppard, D. Fowler, A. F. Harrison, A. O. Parkinson, P. Dao, and **I. S. Paterson**. 1992. Contribution of canopy leaching to sulphate deposition in a Scots pine forest. Environmental Pollution 75: 229-236.

Cappellato, R., N. E. Peters, and **H. L. Ragsdale**. 1993. Acidic atmospheric deposition and canopy interactions of adjacent deciduous and coniferous forests in the Georgia Piedmont. Canadian Journal of Forest Research 23: 1114-1124.

Carlyle-Moses, D. E. Price, and **A. G. Price**. 1999. An evaluation of the Gash interception model in northern hardwood stand. Journal of Hydrology 214: 103-110.

Eaton, J. S., G. E. Likens, and **F. H. Bormann**. 1973. Throughfall and stemflow chemistry in a northern hardwood forest. Journal of Ecology 61: 495-508.

Environment Canada. 1991. The State of Canada's Environment. Ottawa, Ontario: Supply and Services Canada.

Foster, B. A. 1993. The Acid Rain Debate. Science and Special Interests in Policy Formation. Iowa, USA, Iowa State University Press.

Gaber, B. A., and **T. C. Hutchinson.** 1988a. The neutralisation of acid rain by the leaves of four Boreal forest species. Canadian Journal of Botany 66: 1877-1882.

Gaber, B. A., and **T. C. Hutchinson.** 1988b. Chemical changes in simulated raindrops following contact with leaves of four Boreal forest species. Canadian Journal of Botany 66: 2445-2451.

Gash, J. H. C., C. R. Lloyd, C. R. Lachaud, and **G. Lachaud.** 1995. Estimating sparse rainfall interception with an analytical model. Journal of Hydrology 170: 79-86.

Gjengedal, E. 1996. Effects of soil acidification on foliar leaching and retranslocation of metals in vascular plants. Water, Air and Soil Pollution 86: 221-234.

Gough, W. A., C. Lillyman, J. D. Karagatzides, and **L. J. S. Tsuji.** 2002. Determining the validity of using summer monitoring of acid deposition in Southern Ontario, Canada. Water, Air and Soil Pollution, 137: 305-316.

Granat, L., and **J. Hallgren.** 1992. Relation between estimated dry deposition and throughfall in a coniferous forest exposed to controlled levels of SO_2 and NO_2. Environmental Pollution 75: 237-242.

Helvey, J. D., and **J. H. Patric** 1965. Canopy and litter interception of rainfall by hardwoods of Eastern United States. Water Resources Research 1: 93-206.

Houle, D., R. Ouimet, R. Paquin, and **J. Laflamme**. 1999. Interactions of atmospheric deposition with a mixed hardwood and a coniferous forest canopy at the Lake Clair Watershed (Duschenay, Quebec). Canadian Journal of Forest Research 29: 1944-1957.

Howells, G. 1990. Acid rain and acid waters. New York, Ellis Horwood.

Hutchinson, T. C., C. M. Adams, and **B. A. Gaber**. 1986. Neutralization of acidic rainfall on leaves of agricultural crop and Boreal forest species. Water, Air, and Soil Pollution 31: 475-484.

Jiang M., and **R. Jagels**. 1999. Detection and quantification of changes in membrane associated calcium in red spruce saplings exposed to fog. Tree Physiology 19: 909-916.

Kumar, A. J., W. A. Gough, J. D. Karagatzides, K. A. Bolton, and **L. J. S.Tsuji.** 2001. Testing the validity of a critical sulfur and nitrogen load model in southern Ontario, Canada using soil chemistry data from MARYP. Environmental Monitoring and Assessment 69: 221-230.

Liechty, H. O., G. D. Mroz, and **D. D. Reed**. 1993. Cation and anion fluxes in northern hardwood throughfall along an acidic deposition gradient. Canadian Journal of Forest Research 23: 457-467.

Lindberg, S. E., G. M. Lovett, D. D. Richter, and **D. W. Johnson**. 1985. The effects of acidic deposition on cation leaching from three deciduous forest canopies. Canadian Journal of Forest Research 15: 1055-1060.

Lindberg, S. E., G. M. Lovett, D. D. Richter, and **D. W. Johnson**. 1986. Atmospheric deposition and canopy interactions of major ions in a forest. Science 231: 141-145.

Lovett, G. M., S. E. Lindberg, D. D. Richter, and **D. W. Johnson**. 1985. The effects of acidic deposition on cation leaching from three deciduous forest canopies. Canadian Journal of Forest Research 15: 1055-1059.

Mecklenberg, R. A., H. B. Tukey, and **J. V. Morgan**. 1966. A mechanism for the leaching of calcium from foliage. Plant Physiology 41: 610-613.

Ministry of the Environment. 1986. Countdown acid rain: Ontario's acid gas control program for 1984-1994. Ontario, Canada. Ministry of the Environment.

Neary, A. J., and **W. I. Gizyn.** 1994. Throughfall and stemflow chemistry under deciduous and coniferous forest canopies in South-Central Ontario. Canadian Journal of Forest Research 24: 1089-1100.

Potter, C. S. 1991. Nutrient leaching from *Acer rubrum* leaves by experimental acid rainfall. Canadian Journal of Forestry Research 21: 222-229.

Prakasa Rao, P. S., G. A. Momin, P. D. Safai, A. G. Pillai, and **L. T. Khemani**. 1995. Rain water and throughfall chemistry in the silent valley forest in South India. Atmospheric Environment 29: 2025-2029.

Puckett, L. J. 1990. Time and pH-dependent leaching of ions from deciduous and coniferous foliage. Canadian Journal of Forestry Research 20: 1779-1785.

Robson, A. J., C. Neal, G. P. Ryland, and **M. Harrow**. 1994. Spatial variations in throughfall chemistry at the small plot scale. Journal of Hydrology 158: 107-122.

Skeffington, R. A., and **P. M. Sutherland**. 1995. The effects of SO_2 and O_3 fumigation on acid deposition and foliar leaching in the liphook forest fumigation experiment. Plant Cell and Environment 18: 247-261.

Veltkamp, A. C., and **G. P. Wyers**. 1997. The contribution of root-derived sulphur to sulphate in throughfall in a Douglas Fir forest. Atmospheric Environment 31: 1385-1391.

Received 28 May 2001
Accepted 12 April 2004

Comparison of the Ground Vegetation in Spruce Plantations and Natural Forest in the Greater Fundy Ecosystem, New Brunswick

CAM VEINOTTE, BILL FREEDMAN[1], WOLFGANG MAASS, and FRIEDERIKE KIRSTEIN

Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1 Canada
[1] Corresponding author

Veinotte, Cam, Bill Freedman, Wolfgang Maass, and Friederike Kirstein. 2003. Comparison of the ground vegetation in spruce plantations and natural forest in the Greater Fundy ecosystem, New Brunswick. Canadian Field-Naturalist 117(4): 531-540.

We studied changes in ground vegetation associated with the conversion of natural, mature, mixed-species forest into conifer plantations in southeastern New Brunswick. This was done to determine the degree to which plant-associated biodiversity was affected by this forestry practice. Species of lichens, bryophytes, and vascular plants were examined in a 21-year chronosequence of 12 Black Spruce (*Picea mariana*) plantations and compared to 8 stands of natural forest of the type replaced. The richness, diversity, and density of species were greatest during younger stages of the plantation sere, with as many as 170 species occurring in a 6-year-old stand. Species occurred in successional stages according to their abilities to: (a) survive disturbances associated with clear-cutting and plantation establishment; (b) regenerate vegetatively; (c) re-establish from a persistent seedbank; (d) invade disturbed habitat by dispersed seeds; and/or (e) tolerate environmental stress imposed by the overtopping canopy during stand development. Multivariate analyses suggested that successional factors had the strongest influence on differences in the ground vegetation among stands of various ages. Gaps in the canopy of reference forest and older plantations provided microsite conditions similar to those of early seral stages, allowing some ruderal species to persist in older stands. Non-indigenous species were almost entirely limited to younger plantations. Some species of natural forest were rare or absent from plantations and may be at risk from the extensive development of these agroforestry habitats in our study region; these included *Acer pensylvanicum, Cephaloziella* spp., *Chiloscyphus* spp., *Fagus grandifolia, Lepidozia reptans, Nowellia curvifolia, Odontoschisma denudatum*, and *Viburnum alnifolium*

Key Words: forestry, plantations, clear-cutting, plant communities, ground vegetation, environmental impact, New Brunswick.

Of all methods of timber harvesting, clear-cutting causes the greatest change in forest ecosystems. Important effects include: reduction of biomass and nutrient capital (with potential damage to site quality and decreased carbon storage), increased erosion, altered hydrology, and changes in biodiversity at the levels of species, community, and landscape (Anonymous 1986; Freedman et al. 1994; Freedman 1995; Kohm and Franklin 1997; Mallik et al. 1997; Hunter 1999; Lindenmayer and Franklin 2002; Kimmins 2003). The changes in composition and diversity of plant communities after clear-cutting and associated management practices, such as those involving plantation establishment, are influenced by biotic and abiotic qualities of the site and by the colonizing and competitive abilities of particular species (Grime 1979; Smith 1980; Crowell and Freedman 1994; Freedman 1995).

Our study area in southeastern New Brunswick is in a region of the Maritime Provinces and eastern Maine where the natural Acadian (or Northern Appalachian) Forest has been reduced greatly in extent. The reduction is a result of clear-cut logging and plantation establishment, along with wildfire and the development of agricultural, residential, and tourism-related land uses. Our study area is part of the Greater Fundy Ecosystem (GFE), consisting of Fundy National Park a protected area of 206 km^2 plus its nearby surrounding area, which is largely a mosaic of plantations, recent clear-cuts, some agricultural land, and residual stands of natural forest. Within this landscape-scale context, there is a need to conserve indigenous biodiversity, even while extensive tracts are being utilized to support economically important activities, including commercial forestry, agriculture, and tourism. At this scale, it is important to have large protected areas, such as the national park, but also to practise conservation-minded management in tracts that form the dominant "matrix" between protected areas, such as lands used for forestry. If this is to be done, then knowledge is required about the stand- and landscape-level risks to indigenous biodiversity that are associated with management practices, such as the conversion of natural forest into intensively managed forestry plantations.

Although Fundy National Park conserves a large area of natural forest, its ecological integrity is being challenged by anthropogenic stressors (Woodley et al. 1993, 1998; Freedman et al. 1994). There are stressors within the national park associated with extensive tourism-related development and a regionally important highway — these land-uses and related activities have caused habitat loss and stress to native species. For instance, more than 130 non-native plants now occur in the park (Burzynski et al. 1986); their abundance is partly due to agricultural practices occurring before park designation and to ongoing maintenance of grassy habitat around buildings, in campgrounds, and along roads.

In addition, most terrain around and adjacent to the park is being intensively managed for industrial forestry — natural, mixed-species forest has been extensively clear-cut and converted to conifer plantations, greatly changing the ecological character of sites and landscape. In part, this management system has been implemented because of economic damage caused to natural forest by the most recent irruption of Spruce Budworm (*Choristoneura fumiferana*). Although natural forest regenerates well after budworm-caused damage, because of a vigorous advance regeneration of seedlings of fir and spruce, commercial forestry interests often prefer to replace damaged stands with plantations of higher productivity. Stands within the national park are not directly affected by these forestry practices. However, the extensive conversion of natural forest into plantations in the surrounding area may indirectly affect ecosystems and species within the park through habitat diminishment and insularization, changes in hydrology, and other influences.

In the present study, we examined differences in species composition, richness, and diversity in the ground vegetation of spruce plantations of various ages, and compared them with reference stands of natural forest of the type that have been converted into the plantations. The objectives of the study are to: (1) describe successional development of plantations and the growth strategies of key species of plants, bryophytes, and lichens; (2) to identify potential risks to indigenous species; and (3) to determine whether non-native plants are invading the managed habitats.

Materials and Methods

Study Area

Our study area (centered at 45° 66'N and 65° 10'W) is in southeastern New Brunswick, Canada. It is located in the Atlantic Maritime Ecozone (Ecological Stratification Working Group 1995), within the Fundy Plateau Ecodistrict of the Southern Uplands Ecoregion of the Acadian Forest Region (Loucks 1962; Rowe 1972). The natural forest of the ecodistrict is dominated by mixed-species stands of Red Spruce (*Picea rubens*), White Spruce (*P. glauca*), Balsam Fir (*Abies balsamea*), Sugar Maple (*Acer saccharum*), Red Maple (*A. rubrum*), Yellow Birch (*Betula alleghaniensis*), White Birch (*B. papyrifera*), and Mountain Birch (*B. cordifolia*). Extensive disturbances, largely related to natural irruptions of Spruce Budworm, have resulted in most mature natural forest having a mixed-species canopy with patches of regenerating coniferous and angiosperm trees.

Study Sites

Twenty sites of at least 10 hectares were selected for study (Table 1). All sites occur in a relatively small area and are within 4 km of at least one other site. The sites were chosen to be comparable in topography, climate, elevation, site quality, and disturbance history, and to be accessible from the local road network. All sites are well-drained, on broadly flat terrain with no slopes greater than five degrees, and with loamy soil over a parent material of upland glacial till (Woodley, 1985). The soil association is a humo-ferric Lomond podzol (Canada Soil Survey Committee 1978; Maliondo et al. 1990).

Twelve of the study sites were Black Spruce (*Picea mariana*) plantations of various ages (3 to 21 years post-establishment; the latter was the oldest plantation in the area) located within 5 km of Fundy National Park. The plantations were all established by the same forestry company and originated with clear-cutting, site preparation by crushing, planting of spruce seedlings, and a release treatment with herbicide at 3-5 years of age. The other eight sites supported natural, mature, mixedwood forest. These "reference" stands were mostly within the park, but were nevertheless located close to the plantations studied (in several cases, on the opposite side of a boundary road). The reference stands were representative of the mixed-species forest that had been harvested and converted into nearby plantations. Stand age was determined by coring eight dominant and subdominant trees per stand. Although the reference stands were mature at the time of our study, they may have been selectively logged prior to 60-70 years ago (the park was established in 1948) when there were several local sawmills (Burzynski 1985). The selective logging was followed by natural regeneration.

Data Collection

The ground vegetation was sampled in July and August in 1995 or 1996. The sampling was done in 30 quadrats (1 m × 1 m) located randomly along transects. The percent cover of species of vascular plants, bryophytes, and lichens was estimated visually as the proportion of ground surface obscured by a perpendicular projection of the foliage. Because foliage could be layered, total cover could exceed 100%. If cover of a species was less than 1%, it was noted as "present" and assigned a nominal value of 0.1%. After the 30 quadrats were sampled a wider reconnaissance was made over the study site for 20-30 minutes; any additional species found were assigned a value of 0.1% in the community analysis. Taxonomy of vascular plants follows Hinds (2000), while bryophytes follow Crum (1976) and lichens Brodo et al. (2001).

To provide data on habitat and stand structure, living and dead trees (i.e., with diameter at breast height ≥5.0 cm) in reference stands were sampled for DBH in 12 plots of 20 m × 20 m per stand. Because tree distribution and size were relatively homogenous in plantations, they were sampled in fewer (9) plots of a smaller size (10 m × 10 m). Shrub-sized plants were identified and their diameter measured at 25 cm in two 5 m × 5 m subquadrats nested in opposite corners of each tree quadrat (18-24 quadrats per stand). The field data were used to calculate density (stems/ha)

TABLE 1. General description of research stands. TBA is tree basal area (m^2/ha); SBA is shrub basal area (m^2/ha). The data for tree species are relative dominance.

Site Name	Site Description	Dominant Trees
R1	Mature conifer-dominated mixedwood, 60-90 yr old, some budworm damage; TBA 29.3, SBA 1.8	Pr 74%; Bc 11%; Ar 10%; Ba 3%; Bp 1%
R2	Mature mixedwood, 80-130 yr old, some budworm damage; TBA 29.1, SBA 1.9	Pr 58%; Ba 27%; Ar 8%; Bc 6%
R3	Tolerant hardwood, 60 yr old, small-scale, selective logging before 1947; TBA 33.1, SBA 1.1	As 26%; Ba 21%; Pr 17%; Ar 17%; Bc 12%
R4	Mature conifer-dominated mixedwood, 55-140 yr old, extensive budworm damage; TBA 28.0, SBA 2.8	Pr 68%; Ba 16%; Ar 13%; Bc 3%
R5	Mature mixedwood, 60 yr old, some budworm damage; TBA 25.4, SBA 2.4	As 40%; Pr 27%; Ar 12%; Ba 12%; Fg 10%
R6	Mature mixedwood, 55 yr old, some budworm damage; TBA 27.7, SBA 2.8	As 34%; Pr 27%; Ar 18%; Fg 16%; Ba 4%
R7	Mature mixedwood, 60-80 yr old, some budworm damage; TBA 30.5, SBA 0.9	As 50%; Pr 32%; Ba 12%; Ar 6%
R8	Mature conifer-dominated mixedwood, 75-110 yr old, some budworm damage; TBA 28.7, SBA 2.0	Pr 78%; Ba 12%; Bc 5%; Ar 3%; As 2%
P21	21 yr old, clearcut, planted with spruce, TBA 15.1, SBA 1.0	Pm 71%; Ab 28%; Pg 1%
P18	18 yr old, as above; TBA 10.8, SBA 6.2	Pm 73%; Ab 27%
P15	15 yr old, as above; TBA 28.8, SBA 3.2	Pm 78%; Ab 22%
P13	13 yr old, as above; TBA 5.6, SBA 0.7	Pm 79%; Ab 21%
P8	8 yr old, as above; TBA 5.1, SBA 3.7	Ab 58%; Pm 42%; Bc 1%
P7	7 yr old, as above; TBA 0.5, SBA 4.6	No tree-sized plants
P6a	6 yr old, as above; TBA 0.0, SBA 2.0	No tree-sized plants
P6b	6 yr old, as above; TBA 0.3, SBA 4.6	No tree-sized plants
P5a	5 yr old, as above; TBA 0.0, SBA 1.5	No tree-sized plants
P5b	5 yr old, as above; TBA 0.0, SBA 0.9	No tree-sized plants
P4	4 yr old, as above; TBA 0.0, SBA 0.9	No tree-sized plants
P3	3 yr old, as above; TBA 0.0, SBA 0.9	No tree-sized plants

Species code: As = *Acer saccharum*, Ar = *Acer rubrum*, Ba = *Betula alleghaniensis*, Bc = *Betula cordifolia*, Bp = *Betula papyrifera*, Fg = *Fagus grandifolia*, Pm = *Picea mariana*, Pg = *Picea glauca*, Pr = *Picea rubens*.

and basal area (m^2/ha) of trees, snags, and shrubs (only summary data are reported here; the details are in Fleming and Freedman 1998).

Data Analysis

The ground vegetation data for the plantations were analyzed to determine phytosociological changes during the 21-year sere. For some analyses, the species of ground vegetation were divided into nine functional guilds: feather mosses, other bryophytes, lichens, pteridophytes, gymnosperms, monocots, dicot herbs, dicot shrubs, and *Rubus* species. Changes associated with ecological conversion were examined by comparing plantations to reference forest. Species richness was calculated as the number of species encountered at each site. Species density was the average number of species per m^2 quadrat. Species diversity was calculated as the Shannon-Weaver index (Cox 1996): $H' = -\Sigma (p_i \cdot \ln p_i)$, with p_i of each species estimated using relative cover.

Multivariate analyses were used to explore relationships among stands. The data inputs were matrices of understorey species cover by site (Kovach 1995). To avoid undue influence of rare species, only the 79 species having an average cover $\geq 1\%$ in at least one stand were used in the analyses. The analyses were performed using the MultiVariate Statistical Package (MVSP). A hierarchical cluster analysis was used to identify groupings of stands (or "communities"), using a procedure based on reciprocal averaging and divisions based on site attributes, with indicator species identified for the divisions in the classification (Gauch 1982; Kovach 1995). An ordination was performed by detrended correspondence analysis (DCA), which also calculates eigenvalues by a reciprocal averaging procedure; the detrending of the second and higher axes prevents a quadratic dependency, eliminating the potential for an arching effect (Gauch 1982). Compression of the axes is avoided by rescaling, so distances in the ordination space have consistent meaning in terms of compositional differences of samples.

Results and Discussion

Species Richness, Density, and Diversity

Species richness was greatest during the initial stages of the plantation sere, with a maximum of 170 species occurring in a six-year-old plantation (Table 2). Species richness then decreased to lower values in the oldest plantations, ranging from 98-112 species in stands

TABLE 2. Ground vegetation species richness, density, and diversity in plantations and reference stands. The age of the reference stands is approximately 70 years.

Stand	Age (years)	Species Richness (total species/site)	Species Density (species/m^2)	Species Diversity (Shannon-Weaver)
P3	3	135	11.4	2.99
P4	4	120	13.4	3.17
P5a	5	146	16.2	3.53
P5b	5	77	16.3	2.71
P6a	6	170	17.6	3.10
P6b	6	128	18.8	3.34
P7	7	141	20.9	3.46
P8	8	124	18.1	3.18
P13	13	98	18.7	2.40
P15	15	112	15.1	2.85
P18	18	80	11.5	2.39
P21	21	98	11.9	2.27
R1	70	92	13.1	2.97
R2	70	141	17.4	3.33
R3	70	98	10.8	2.62
R4	70	92	14.5	2.80
R5	70	102	14.6	2.35
R6	70	100	14.4	2.94
R7	70	74	11.1	2.46
R8	70	93	11.3	3.00

13-21 years old. Values similar to the oldest plantations occurred in mature reference stands (average of 99 species; the range was generally 74 to 102 species, with reference site two (R2) anomalous with 141 species).

Shannon-Weaver diversity ranged from 2.71 to 3.52 in plantations aged 3 to 8 years old (Table 2). Species diversity generally decreased through the plantation chronosequence, with the lowest value observed in the oldest stand, while reference stands ranged from 2.35 to 3.33.

The higher species richness and diversity in young plantations is due to their relatively open conditions and the spatial heterogeneity of environmental factors and vegetation (Shafi and Yarranton 1973; Crowell and Freedman 1994). Other studies have reported relatively high richness and diversity of ground vegetation during the initial stages of succession after timber harvesting, followed by a large decline as more shaded conditions develop (Shafi and Yarranton 1973; Bormann and Likens 1979; Hibbs 1983; Schoonmaker and McKee 1988; Burton 1989; Reiners 1992; Crowell and Freedman 1994; Gilliam et al. 1995; Qi and Scarratt 1998; Roberts and Methven 1998). It has been suggested that the highest diversity of trees occurs in intermediate regenerative conditions, as this transitional period contains both early- and later-successional species (Loucks 1970; Auclair and Goff 1971; Pickett 1976; Connell 1978). In the understorey, however, competitive exclusion of intolerant species occurs earlier in succession because of the rapid development of a shading overstorey.

Species density was lowest in the youngest plantation surveyed (three years old), where it was 11.4 spp./m^2 (Table 2). It increased to 20.9 spp./m^2 in a seven-year plantation and then decreased and leveled off at 11.5-11.9 spp./m^2 in older stands. Species density in reference sites generally ranged from 10.8 to 14.6 spp./m^2 (average 13.4 spp/m^2), with site R2 again anomalous with 17.4 spp./m^2. The lowest species density among reference stands was in a tolerant hardwood stand dominated by a closed canopy of Sugar Maple. Although species density is an infrequent variable in ecological studies, it was also reported by Reiners (1992) to increase during the initial years of natural regeneration after forest harvesting, peaking in a five-year-old stand.

Changes in Cover

The total cover of ground vegetation initially increased rapidly with plantation age. However, the highest values occurred in plantations aged 13 years (130%) and 21 years (140%), while the 18-year-old stand had a relatively low cover (43%). The total cover in reference stands (average 68%; range 40-98%) was lower than in most plantations. Studies of natural regeneration after the clear-cutting of temperate hardwood or mixedwood forest have shown that an approximately complete foliar canopy of herbaceous and shrub-sized plants can re-establish within only 4-6 years of disturbance, casting substantial shade over the forest floor (Bormann and Likens 1979; Burton 1989; Crowell and Freedman 1994). As the over-topping canopy of shrubs and trees further develops, there is a substantial decline in lower-growing plants of the ground vegetation.

The most abundant species in the ground vegetation of plantations aged 3 to 8 years old (listed in order of

decreasing average cover) were: *Cornus canadensis*, *Rubus strigosus*, *Picea mariana*, *Sphagnum girgensohnii*, *Polytrichum commune*, *Epilobium angustifolium*, *Solidago graminifolia*, and *Agrostis scabra*. In plantations aged 13 to 21 years the most abundant species were: *Picea mariana*, *Cornus canadensis*, *Pleurozium schreberi*, *Vaccinium myrtilloides*, *Polytrichum commune*, *Calamagrostis canadensis*, *Abies balsamea*, and *Betula cordifolia*. Reference stands were dominated by: *Dryopteris campyloptera*, *Dryopteris spinulosa*, *Cornus canadensis*, *Oxalis montana*, *Dennstaedtia punctilobula*, *Abies balsamea*, *Maianthemum canadense*, and *Viburnum alnifolium*.

The most frequently encountered species in plantations aged 3 to 8 years old were: *Rubus strigosus*, *Cornus canadensis*, *Maianthemum canadense*, *Agrostis scabra*, *Picea mariana*, *Cladonia* spp., *Pleurozium schreberi*, and *Solidago graminifolia*. In plantations aged 13 to 21 years the most frequent taxa were: *Cornus canadensis*, *Pleurozium schreberi*, *Picea mariana*, *Maianthemum canadense*, *Cladonia* spp., *Dicranum ontariense*, and *Polytrichum commune*. The most frequent species in reference stands were: *Maianthemum canadense*, *Oxalis montana*, *Dryopteris spinulosa*, *Cornus canadensis*, *Hypogymnia physodes*, *Dryopteris campyloptera*, and *Acer rubrum*.

The overall successional pattern of species composition in plantations is one of increasing tolerance of the stressful conditions occurring beneath the developing overstorey (see Sparling 1967; Crowell and Freedman 1994; Freedman 1995). Species with the greatest prominence in younger plantations (up to 8 years old) varied in their ability to tolerate shading, as these stands included both ruderal invaders (such as *Agrostis scabra*, *Epilobium angustifolium*, *Polytrichum commune*, and *Solidago graminifolia*) and more tolerant ones that survived the disturbance event (e.g., *Cornus canadensis*, *Maianthemum canadense*, *Picea mariana*, and *Pleurozium schreberi*). Older plantations (13 to 21 years) contained fewer intolerant species and they were much less abundant. Although most species of the mature natural forest are shade tolerant, some intermediate and even intolerant plants occurred in open, patchy microhabitats associated with gap-phase disturbances (notably *Rubus strigosus*). Most of the reference stands had been affected by past infestations of Spruce Budworm, which caused selective mortality of mature balsam fir and spruce and created gaps in the canopy. Ruderal plants grew in these relatively open microhabitats; during microsuccession they are replaced by more competitive species.

Raspberry exemplifies elements of both the ruderal and competitor growth strategies (Grime 1979). After destruction of the overstorey by clear-cutting, *Rubus* species rapidly achieved prominence in the regenerating ground vegetation, mostly by the establishment of seedlings from a persistent seedbank (Grignon 1992). *Rubus strigosus*, the most abundant *Rubus* in our study, achieved its greatest cover within six years of the disturbance. The inability of *Rubus* spp. to tolerate shade soon resulted in a large reduction in its abundance (Whitney 1978; Grignon 1992; Archambault et al. 1998). However, *Rubus* species persisted in a small abundance within gap-disturbance microhabitats in older plantations and natural forest.

Non-Native Species

The great majority of vascular plants encountered within the plantation chronosequence are indigenous, as are all of the abundant species noted above. Although plantations supported some non-native plants (average of 4.9 species encountered per site; range 2-9 spp./site), their presence is ephemeral because these shade-intolerant ruderals became greatly diminished after an over-topping canopy developed (Table 3; there was a negative correlation (t-test; $p<0.005$) between plantation age and relative cover of non-indigenous plants). Almost all non-native plants colonized the plantations through wind dispersal and exhibited a ruderal growth strategy. Reference stands had a much smaller frequency and cover of non-native species than plantations.

Indicator Species of Reference Forest

Although relatively few stands were surveyed in this study ($n = 20$), some species were found only in reference forest. These were: *Acer pensylvanicum*, *Cephaloziella* spp., *Chiloscyphus* spp., *Fagus grandifolia*, *Lepidozia reptans*, *Nowellia curvifolia*, *Odontoschisma denudatum*, and *Viburnum alnifolium* (see also Roberts and Methven 1998). These species may be considered indicators of the natural forest condition in our study region, and may potentially be at risk from extensive conversions of natural forest into plantations. However, none of the vascular plants encountered within this study is considered rare in New Brunswick (Hinds 1983).

The needs of these species may be accommodated by the use of "softer," less intensive management practices that favour their survival, such as shelterwood and selection harvesting (Atlegrim and Sjoberg 1996; Hannerz and Hanell 1997). However, more research on these less intensive systems must be undertaken to better understand how they affect understorey plants.

Changes in Functional Guilds

To aid in the interpretation of changes associated with succession and conversion in our extremely complex dataset, which consists of a matrix of 170 species by 20 sites, the ground vegetation was divided into the following functional guilds: feather mosses, other bryophytes, lichens, pteridophytes, gymnosperms, monocots, dicot herbs, dicot shrubs, and *Rubus* species (Table 4).

Feather mosses (mostly *Pleurozium schreberi* and *Hylocomium splendens*) occurred in low abundance during the initial 13 years of the plantation chronosequence, with average cover ranging from <0.1% to

TABLE 3. Non-native plants in plantations and natural forest. Numbers in brackets refer to the frequency of occurrence within stands of the indicated age-class.

Plantations aged 3-8 years (n = 8)	Plantations aged 13-21 years (n = 5)
Agrostis capillaris (13)	*Agrostis tenuis (80)*
Agrostis stolonifera (88)	*Agrostis stolonifera (40)*
Agrostis tenuis (63)	*Bromus secalinus (20)*
Bromus secalinus (50)	*Chrysanthemum leucanthemum (20)*
Carex leporina (13)	*Cirsium arvense (20)*
Cirsium arvense (13)	*Cirsium vulgare (20)*
Cirsium vulgare (25)	*Galeopsis tetrahit (20)*
Galeopsis tetrahit (63)	*Hieracium caespitosum (20)*
Festuca tenuifolia (13)	*Hypericum perforatum (20)*
Hieracium aurantiacum (25)	*Poa pratense (20)*
Hieracium caespitosum (50)	*Ranunculus acris (20)*
Hieracium florentinum (13)	*Rumex acetosella (20)*
Hieracium pilosella (38)	*Tanacetum vulgare (20)*
Phleum pratense (13)	
Poa compressa (13)	Mature reference stands (n = 8)
Poa pratense (25)	*Agrostis palustris* (13)
Polygonum hydropiper (50)	*Agrostis tenuis* (13)
Populus alba (13)	
Potentilla recta (13)	
Ranunculus acris (13)	
Rumex acetosella (87)	
Rumex crispus (13)	
Senecio jacobaea (13)	
Stellaria graminifolia (13)	

2.5% (Tables 4, 5). Feather mosses increased in older plantations, attaining 49% cover in the 21 year-old stand. Their cover in reference stands generally ranged from 0.0 to 2.9% (site R2 was anomalous with 8.5%). The growth of feather mosses is facilitated by moist, shaded, acidic conditions, and they may develop an almost continuous carpet beneath a dense conifer canopy (Foster 1985; personal observations). In our study, feather mosses that survived clear-cutting were unable to tolerate the heat and dryness of the aftermath conditions, so this guild was sparse in the youngest plantations. Feather mosses then increased as the canopy closed, achieving their highest cover in the oldest plantation surveyed (21 years), in which a dense canopy prevented much sunlight from reaching the forest floor. It is likely that the abundance of feather mosses would increase further as the plantations develop towards their anticipated rotation age of about 40 years. The reference stands had a relatively open canopy and less dominance by conifer trees, and feather mosses occurred only in patches of suitable microhabitat.

Other bryophytes (i.e., excluding feather mosses) were ubiquitous in the chronosequence, reflecting the wide range of environmental conditions suitable for the diverse species in this guild. They increased during the plantation succession, reaching 67.5% cover in the 21-year stand. Their average cover in reference stands was less than in plantations. Species in the youngest plantations were mostly those capable of surviving the initial disturbance and its aftermath conditions, especially *Polytrichum* spp. (Foster 1985). *Polytrichum* species were also most abundant in the oldest plantations studied.

Lichens maintained a relatively low abundance through the plantation chronosequence, but increased somewhat to a maximum of 3.1% in a 15 year-old-stand. The lichen cover of reference stands ranged from 0.6 to 1.8%. These observations reflect the inherently slow colonization and growth rates of this group (Hale 1974).

Pteridophytes occurred in the youngest and oldest plantations surveyed and had their maximum cover (14%) in a 13-year-old stand. Pteridophyte cover was higher in reference stands, averaging 28% (range 11 to 47%). The initial increase during succession is likely a result of vegetative expansion via rhizomes (Cody et al. 1977).

Gymnosperms increased greatly during the chronosequence to a maximum of 39% in a 13-year plantation. After this time most of the gymnosperm component grew into shrub- and tree-sized elements, which were not recorded within the lower-growing ground vegetation. (The overhead canopy of conifers increased greatly in older plantations; Fleming and Freedman 1998). The abundance of gymnosperms is due to the plantations being planted with seedlings of Black Spruce, along with the survival and growth of an abundant advance regeneration of small Balsam Fir and

TABLE 4. Average cover (%) of functional guilds in a chronosequence of spruce plantations and in reference forest.

Guild	P3	P4	P5a	P5b	P6a	P6b	P7	P8	P13	P15	P18
Feather mosses	0.0	0.1	0.6	0.2	1.8	0.2	2.3	0.4	2.5	13.3	14.1
Other bryophytes	13.0	11.3	20.5	16.8	15.1	21.0	17.2	18.1	8.7	32.6	23.5
Lichens	0.4	0.8	2.2	2.3	1.4	0.0	1.1	1.3	2.7	3.1	1.9
Pteridophytes	0.3	3.1	0.5	1.0	4.9	0.7	4.1	2.7	14.3	0.0	0.7
Gymnosperms	1.5	8.7	6.3	7.4	9.1	0.7	9.9	19.6	39.0	31.3	0.0
Monocots	6.5	8.2	11.9	7.5	6.8	17.3	11.2	16.1	2.7	15.3	1.9
Dicot herbs	24.7	24.7	33.1	30.9	35.8	24.2	27.6	34.8	48.0	10.8	12.6
Dicot shrubs	4.1	2.2	3.8	2.6	10.5	2.2	5.3	8.6	9.8	12.0	2.5
Rubus species	6.4	9.8	8.3	11.8	21.0	15.1	13.8	8.9	4.9	0.5	0.3
TOTAL COVER	56.7	68.7	86.6	80.3	104.5	81.3	90.1	110.0	130.0	105.5	43.3

Guild	P21	R1	R2	R3	R4	R5	R6	R7	R8	Ref avg.
Feather mosses	49.4	0.1	8.5	0.0	0.3	1.1	0.1	2.7	2.9	2.0
Other bryophytes	67.5	2.5	17.6	2.9	5.9	9.2	3.0	9.1	9.1	7.4
Lichens	0.5	0.7	1.8	0.6	1.0	1.4	0.9	0.8	1.0	1.0
Pteridophytes	4.8	26.2	22.3	36.2	40.9	47.1	22.1	21.0	11.0	28.4
Gymnosperms	18.6	0.6	8.0	0.2	4.1	2.9	2.7	8.9	3.7	3.9
Monocots	0.4	7.7	0.1	3.3	3.3	1.8	1.6	2.6	0.3	2.6
Dicot herbs	18.0	9.0	24.4	8.1	16.8	26.7	8.4	12.9	11.2	14.7
Dicot shrubs	28.6	16.6	8.1	8.7	14.2	7.9	15.1	1.3	2.7	9.3
Rubus species	1.2	0.3	2.3	0.3	0.8	0.8	1.2	0.1	1.3	0.9
TOTAL COVER	139.6	63.6	84.5	60.2	87.0	97.8	54.9	56.8	40.3	68.1

Red and White spruce (Anonymous 1965; Freedman 1995). In reference stands, gymnosperm cover ranged from 0.2 to 9% (average 4%).

Monocots had a relatively high cover in younger plantations, with up to 17% in a 6-year-old stand. Some species (e.g., *Carex trisperma*) survived the initial disturbance event, while others (e.g., species of *Agrostis*) invaded the site afterward and were prominent in younger and intermediate seral stages. In reference stands monocots occurred at smaller but variable levels, averaging 2.6%.

Dicot herbs were the most prominent element of the ground vegetation during the first years after plantation establishment, peaking in the 13-year-old plantation at 48% cover, with lower levels in reference stands (average 15%). This mostly reflects species that seeded

TABLE 5. Cover values (%) of the 17 most frequently encountered species by stand age. Where replicate stands (same age) were surveyed, the average is presented.

Stand Age:	3	4	5	6	7	8	13	15	18	21	Reference
Abies balsamea	0.2	4.3	1.2	0.2	4.3	4.1	5.3	1.7	0.0	0.4	2.3
Acer rubrum	0.5	0.0	0.9	0.7	0.2	1.8	2.8	0.0	0.3	0.0	1.2
Agrostis scabra	1.2	2.3	3.4	3.1	2.1	0.2	0.1	0.0	0.0	0.0	0.0
Cornus canadensis	0.0	13.0	34.0	11.0	8.6	23.0	42.0	7.0	12.0	14.0	8.0
Dennstaedtia punctilobula	0.1	0.1	0.0	1.3	0.1	1.3	5.3	0.0	0.0	0.0	2.3
Dryopteris campyloptera	0.0	0.0	0.0	0.2	0.0	0.0	3.2	0.0	0.0	0.0	14.0
Dryopteris spinulosa	0.2	0.4	0.5	0.3	1.0	0.2	3.9	0.0	0.5	0.0	8.4
Maianthemum canadense	0.8	1.0	1.2	0.3	1.1	0.5	1.3	2.6	0.2	0.2	1.9
Oxalis montana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7
Picea mariana	0.0	4.3	5.6	4.6	5.5	15.0	33.0	23.0	0.0	18.0	0.0
Pleurozium schreberi	0.0	0.1	0.2	1.0	2.3	0.4	2.5	13.0	14.0	45.0	1.6
Polytrichum commune	7.0	2.1	2.8	3.1	5.0	8.6	3.5	1.1	0.0	12.0	0.2
Polytrichum formosum	0.0	3.5	3.3	3.9	4.7	0.6	0.1	2.1	1.0	1.8	0.1
Rubus striogosus	6.0	7.1	5.7	17.0	12.0	8.3	4.9	0.4	0.0	0.7	0.5
Solidago graminifolia	0.1	4.9	2.1	3.2	3.3	1.4	0.1	0.0	0.0	0.0	0.0
Solidago rugosa	1.5	0.1	0.6	2.3	2.3	1.5	0.7	2.3	0.1	0.0	0.3
Sphagnum girgensohnii	2.3	3.8	7.8	4.5	2.0	3.2	0.1	3.5	0.7	0.0	1.4

into the disturbed sites, including asters (*Aster* spp., especially *A. umbellatus*), goldenrods (*Solidago* spp., especially *S. rugosa*), and fireweed (*Epilobium angustifolium*). These forbs declined rapidly after an overtopping canopy developed (Freedman 1995).

Dicot shrubs increased in cover with plantation age, with a maximum of 29% in the 21-year plantation, while reference stands ranged from 8 to 27% (average 15%). The average cover of *Rubus* species (mostly *R. strigosus*) was highest (21%) in a 6-year plantation, followed by a decline in older plantations. *Rubus* cover averaged 0.9% in reference sites. The destruction of the overstorey by clear-cutting stimulated a long-lived seedbank of certain species to germinate (particularly Red Elderberry, *Sambucus racemosa*; Pin-Cherry, *Prunus pensylvanica*; and Raspberry, *Rubus* spp., especially *R. strigosus*). In addition, some woody plants that survived the disturbance then regenerated vigorously by stump-sprouting (e.g., Red Maple, *Acer rubrum*, and Beech, *Fagus grandifolia*) (Anonymous 1965; Lees 1981; Beatty 1991; Crowell and Freedman 1994; Qi and Scarratt 1998).

Multivariate Analyses

The cluster analysis identified five natural groupings or "communities" among the 20 stands surveyed (Figure 1). Clusters were largely based on attributes related to stand age and on plantation versus natural forest. Variation not accounted for by the cluster analysis may be due to the influence of site factors we did not study, such as spruce-budworm dynamics, topography, elevation, microclimate, and soil (Roberts and Methven 1998). The five community types identified are:

- Group 1: Older plantations, aged 13, 15, and 21 years since establishment
- Group 2: Reference stands (except for R2; see below)
- Group 3: Middle-aged plantations (5, 6, and 8 years old)
- Group 4: An 18-year-old plantation and a reference stand (R2)
- Group 5: The youngest plantations (3, 4, 5, 6, and 7 years-old)

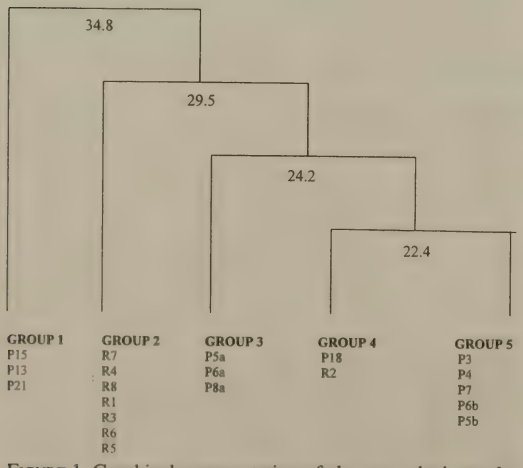


FIGURE 1. Graphical representation of cluster analysis results for 8 reference stands and 12 plantations. The analysis was based on the average cover of species of lichens, bryophytes, and vascular plants in the ground vegetation. Numbers represent eigenvalues.

Axes 1 and 2 of the detrended correspondence analysis accounted for 19.7% and 12.6%, respectively, of the observed variance, while axes 3 and 4 accounted for only 5.2% and 2.3%, respectively, and provided no obvious ecological interpretation. Axes 1 and 2 separated reference stands (situated on the right-hand side of the plot) from plantations (to the left; Figure 2). The plantations are generally ordered according to age. Stands tended to ordinate with their "community" according to the cluster analysis, suggesting a robust analysis in terms of successional and conversion factors being the primary influences on differences in ground vegetation among stands in our study.

Conclusions

The clear-cutting of natural, mixed-species forest followed by plantation establishment initiates a vigorous regeneration of the ground vegetation and a reorganization of its communities. Species inhabit temporally varying habitats in the plantation chronosequence, depending on their abilities to survive the disturbance, colonize the site, take advantage of a temporary flush of resources, and/or tolerate intensifying ground-level stress as the overstorey develops. However, extensive plantation development results in increasingly fewer habitats suitable for species that grow preferentially or exclusively in older, natural forest. This may limit the ability of those species to maintain viable populations within an intensively managed landscape. More research is needed to identify species that are vulnerable to extensive forestry-related habitat conversions, and to provide information necessary to accommodating their needs by changing the management system and by designating a comprehensive system of protected areas. These vulnerable species are also potentially useful in monitoring programs as indicators of ecological integrity and of the sustainability of forestry operations (Woodley et al. 1993; Biodiversity Science Assessment Team 1994; Freedman et al. 1997).

Acknowledgments

This study was supported by research grants to B. Freedman from the Natural Sciences and Engineering Research Council of Canada and the Greater Fundy Ecosystem Research Group, by a research contract from the Fundy Model Forest, and by a Dalhousie University Graduate Fellowship to C. Veinotte. Additional support was provided by Parks Canada and the staff of Fundy National Park. J. D. Irving Forest Products Limited allowed access to their plantations and provided information regarding management prac-

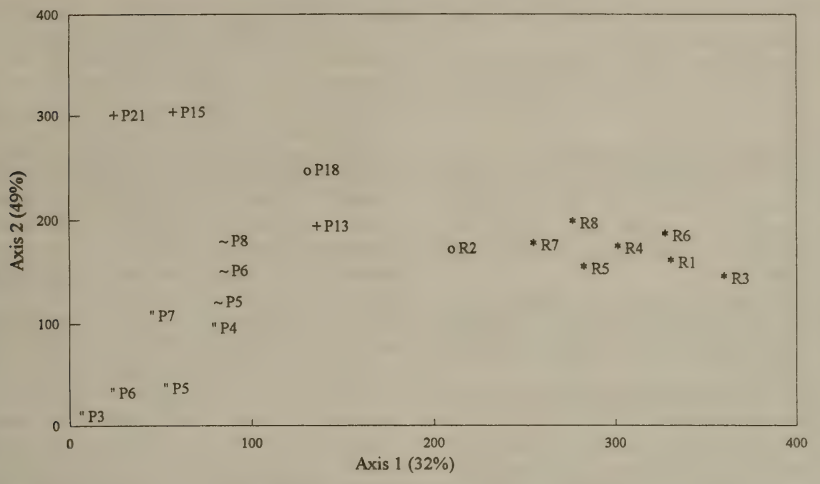


FIGURE 2. Stand scores of axes 1 and 2 of the detrended correspondence analysis (8 reference stands and 12 plantations). "P" and "R" denote plantation and reference stands, respectively. Symbols correspond to the group or "community" to which stands were assigned by the cluster analysis, where: + is Group 1, * is Group 2, ~ is Group 3, o is Group 4, and " is Group 5.

tices. We are also grateful to Tracy Fleming, Jonathan Freedman, Greg Johnson, and Kathleen O'Sullivan for their assistance with fieldwork. Nick Hill of Mount St. Vincent University provided comments on an early draft.

Literature Cited

Anonymous. 1965. Silvics of Forest Trees of the United States. Agricultural Handbook (271), USDA Forest Service, Washington, D.C.

Anonymous. 1986. Ecological effects of clear-cutting. Pages 345-357 *in* Ecological Knowledge and Environmental Problem-Solving. Concepts and Case Studies. Committee on the Applications of Ecological Theory to Environmental Problems. National Academy Press, New York.

Auclair, A. N., and **F. G. Goff**. 1971. Diversity relations in the upland forests of the western Great Lakes area. American Naturalist 105: 499-528.

Archambault, L., J. Morissette, and **M. Bernier-Cardou**. 1998. Forest succession over a 20-year period following clearcutting in balsam fir-yellow birch ecosystems of eastern Quebec, Canada. Forest Ecology and Management 102: 61-74.

Atlegrim, O. and **K. Sjoberg**. 1996. Response of bilberry (*Vaccinium myrtillus*) to clear-cutting and single-tree selection harvests in uneven-aged boreal *Picea abies* forests. Forest Ecology and Management 86: 39-50.

Beatty, S. W. 1991. Colonization dynamics in a mosaic landscape: The buried seed pool. Journal of Biogeography 18: 553-563.

Biodiversity Science Assessment Team. 1994. Biodiversity in Canada: A science assessment for Environment Canada. Environment Canada, Ottawa, Ontario.

Bormann, F. H., and **G. E. Likens**. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York.

Brodo, I. M., S. D. Sharnoff, and **S. Sharnoff**. 2001. Lichens of North America. Yale University Press, New Haven, Connecticut.

Burton, S. M. 1989. Vegetation changes in a post-clear-cutting succession of mixedwood and softwood forests in Nova Scotia. M.Sc. thesis, Dalhousie University, Halifax, Nova Scotia.

Burzynski, M. P. 1985. A guide to Fundy National Park. Douglas & McIntyre, Vancouver, British Columbia.

Burzynski, M. P., S. J. Woodley, and **A. Marceau**. 1986. The vascular flora of Fundy National Park, New Brunswick. New Brunswick Museum, Publications in Natural Science (4), Saint John, New Brunswick.

Canada Soil Survey Committee. 1978. The Canadian System of Soil Classification. Agriculture Canada, Canadian Soil Survey Committee, Publication 1646, Ottawa, Ontario.

Cody, W. J., I. V. Hall, and **C. W. Crompton**. 1977. The biology of Canadian weeds. 26. *Dennstaedtia punctilobula* (Michx.) Moore. Canadian Journal of Plant Science 57: 1159-1168.

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science 199: 1302-1310.

Cox, G.W. 1996. Laboratory Manual of General Ecology, 7th Edition. Wm. C. Brown Publishers, Chicago.

Crowell, M., and **B. Freedman.** 1994. Vegetation development in a hardwood-forest chronosequence in Nova Scotia. Canadian Journal of Forestry Research 24: 260-271.

Crum, H. 1976. Mosses of the Great Lakes Forest. University of Michigan, Ann Arbor.

Ecological Stratification Working Group. 1995. A National Ecological Framework for Canada. Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Hull, Quebec.

Fleming, T. L., and **B. Freedman.** 1998. Conversion of natural, mixed-species forests to conifer plantations: Implications for dead organic matter and carbon storage. Ecoscience 5: 214-221.

Foster, D. R. 1985. Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of south-eastern Labrador, Canada. Journal of Ecology 73: 517-534.

Freedman, B. 1995. Environmental Ecology, 2nd edition. Academic Press, San Diego, California.

Freedman, B., S. Woodley, and **J. Loo**. 1994. Forestry practices and biodiversity, with particular reference to the Maritime provinces of eastern Canada. Environmental Reviews 2: 33-77.

Freedman, B., S. Woodley, and **G. Forbes**. 1997. The Greater Fundy Ecosystem: Planning for an ecologically sustainable landscape. Pages 114-118 *in* Protected Areas in Our Modern World. Proceedings of a Workshop Held as Part of the IUCN World Conservation Congress, Montreal, Que., October, 1996.

Gilliam, F. S., N. L. Turrill, and **M. B. Adams**. 1995. Herbaceous-layer and overstorey species in clear-cut and mature central Appalachian hardwood forests. Ecological Applications 5: 947-955.

Grime, J. P. 1979. Plant Strategies and Vegetation Processes. John Wiley & Sons, New York.

Gauch, H. G. 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, Cambridge, UK.

Grignon, T. G. 1992. The Dynamics of *Rubus strigosus* (Michx.) in Post-Clearcut Mixedwood and Softwood Forests of Nova Scotia. M.Sc. thesis, Dalhousie University, Halifax, Nova Scotia.

Hale, M. 1974. The Biology of Lichens. Wm. C. Brown Publishers, Iowa.

Hannerz, M., and **B. Hanell**. 1997. Effects on the flora in Norway spruce forests following clearcutting and shelterwood cutting. Forest Ecology and Management 90: 29-49.

Hibbs, D. E. 1983. Forty years of forest succession in central New England. Ecology 64: 1394-1401.

Hinds, H. 1983. The Rare Vascular Plants of New Brunswick. Syllogeus 50, National Museums of Canada, Ottawa, Ontario.

Hinds, H. 2000. Flora of New Brunswick, 2nd edition. University of New Brunswick, Fredericton.

Hunter, M. L. 1999. Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK.

Kimmins, J. P. 2003. Forest Ecology: A Foundation for Sustainable Management, 3rd edition. Prentice Hall College Division, Menlo Park, California.

Kohm, K., and **J. F. Franklin**. *Editors*. 1997. Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington, D.C.

Kovach, W. L. 1995. MultiVariate Statistical Package (MVSP) Plus, Version 2.2d. Kovach Computing Services, Wales, UK.

Lees, J. C. 1981. Three generations of red maple stump sprouts. Canadian Forestry Service, Information Report M-X-119. Fredericton, New Brunswick.

Lindenmayer, D. B., and **J. F. Franklin**. 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press, Washington, D.C.

Loucks, O. L. 1962. A forest classification for the Maritime Provinces. Proceedings of the Nova Scotia Institute of Science 25: 85-167.

Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. American Zoologist 10: 17-25.

Maliondo, S. M., M. K. Mahendrappa, and **G. D. Van Raalte**. 1990. Distribution of biomass and nutrients in some New Brunswick forest stands: Possible implications of whole-tree harvesting. Canadian Forestry Service, Information Report M-X-170E/F. Fredericton, New Brunswick.

Mallik, A. U., F. W. Bell, and **Y. Gong.** 1997. Regeneration behavior of competing plants after clear cutting: implications for vegetation management. Forest Ecology and Management 95: 1-10.

Pickett, S. T. A. 1976. Succession: An evolutionary interpretation. American Naturalist 110: 107-119.

Qi, M., and **J. B. Scarratt**. 1998. Effect of harvesting method on seed bank dynamics in a boreal mixedwood forest in northwestern Ontario. Canadian Journal of Botany 76: 872-883.

Reiners, W. A. 1992. Twenty years of ecosystem reorganization following experimental deforestation and regrowth suppression. Ecological Monographs 62: 503-523.

Roberts, M. R., and **I. R. Methven**. 1998. Effects of forestry practices on species composition and taxonomic and structural diversity. Pages 83-85 *in* State of the Greater Fundy Ecosystem. *Edited by* S. Woodley, G. Forbes, and A. Skibicki. Greater Fundy Ecosystem Research Group, University of New Brunswick, Fredericton, New Brunswick.

Rowe, J. S. 1972. Forest Regions of Canada. Canadian Forestry Service, Ottawa, Ontario.

Schoonmaker, P., and **A. McKee**. 1988. Species composition and diversity during secondary succession of coniferous forests in the Western Cascade Mountains of Oregon. Forest Science 34: 960-979.

Shafi, M. I., and **G. A. Yarranton**. 1973. Diversity, floristic richness, and species evenness during a secondary (post-fire) succession. Ecology 54: 897-902.

Smith, R. L. 1980. Ecology and Field Biology, 3rd edition. Harper and Row Publishers, New York.

Sparling, J. H. 1967. Assimilation rates of some woodland herbs in Ontario. Botanical Gazette 128: 160-168.

Whitney, G. G. 1978. A Demographic Analysis of *Rubus idaeus* L. and *Rubus pubescens* Raf. The Reproductive Traits and Population Dynamics of Two Temporally Isolated Members of the Genus *Rubus*. Ph.D. dissertation, Yale University, Connecticut.

Woodley, S. J. *Editor*. 1985. Fundy National Park: Resource Description and Analysis. Parks Canada, Halifax, Nova Scotia.

Woodley, S., G. Forbes, and **A. Skibicki**. 1998. State of the Greater Fundy Ecosystem. Greater Fundy Ecosystem Research Group, University of New Brunswick, Fredericton, New Brunswick.

Woodley, S., J. Kay, and **G. Francis**. 1993. Ecological Integrity and the Management of Ecosystems. Heritage Resource Centre, University of Waterloo, Ontario.

Received 27 August 2001
Accepted 15 April 2004

Movement of Lake Sturgeon, *Acipenser fulvescens*, in a Natural Reach of the Ottawa River

TIM HAXTON

Southern Science and Information Section, Ontario Ministry of Natural Resources, Postal Bag 2002, 10 Campus Road, Kemptville, Ontario K0G 1J0 Canada

Haxton, Tim. 2003. Movement of Lake Sturgeon, *Acipenser fulvescens*, in a natural reach of the Ottawa River. Canadian Field-Naturalist 117(4): 541-545.

A radio-telemetry project was conducted on four Lake Sturgeon in a natural reach of the Ottawa River, Canada. The objective was to ascertain the extent of their movement within a natural river reach. Lake Sturgeon displayed high fidelity to a basin and did not move extensive distances. Maximum distance traveled between tracking locations was 10 km and mean home range was 1528 ha. Mean distance moved did not significantly differ between seasons. Mean water depth in which Lake Sturgeon were located was 3.5 m. Lake Sturgeon were not located within 52 km of the upstream dam.

Key Words: Lake Sturgeon, *Acipenser fulvescens*, radio-telemetry, Ottawa River, Ontario.

Lake Sturgeon, *Acipenser fulvescens,* are endemic to North America and have declined across their range (Williamson 2003). Populations, once abundant in the Great Lakes, are estimated to be <1% of historical levels (Tody 1974 as cited in Caswell et al. 2004). Commercial harvest has been considered the primary cause for their precipitous decline (Harkness and Dymond 1961); however, other stressors such as pollution, habitat degradation, and dam construction have had an impact (Harkness and Dymond 1961; Houston 1987). Dams block migration routes up tributaries to historical spawning areas (Harkness and Dymond 1961; Priegel and Wirth 1971).

Lake Sturgeon are potamodromous, migrating in excess of 200 km (Kempinger 1988; Rusak and Mosindy 1997; Auer 1999) primarily for breeding purposes (Dumont et al. 1987; Auer 1996; McKinley et al. 1998). Migrations generally end at the base of dams in controlled rivers (Auer 1996; D'Amours et al. 2001). Post-spawning migrations are generally back to foraging areas (McKinley et al. 1998). Lake Sturgeon have been found to utilize entire reaches in a controlled river (McKinley et al. 1998). Is this similar for all rivers?

Lake Sturgeon are present in the Ottawa River (Haxton 2002), an altered system with hydro-electric dams constructed along it course. There are several river reaches within the waterbody that are not impounded ("natural"). The objective of this study was to determine the extent of movement by Lake Sturgeon in a natural reach of the Ottawa River over a two-year period and, in particular, if they moved throughout the reach. Also of interest was dams whether impeded further movement. If so, then Lake Sturgeon would be tracked in the vicinity of the dam.

Study Site

The study was based in Allumette Lake of the Ottawa River; a river that has undergone extensive development for hydro-electric purposes (Haxton and Chubbuck 2002). Allumette Lake is approximately 70 km in length, delineated on the southeast by the interprovincial bridge on Highway 148 located downstream of Pembroke (Figure 1) and on the northwest by the Rapides des Joachims power generating station at Rolphton 235 road km upstream from Ottawa. Water depths average 10 to 15 m in this section with a maximum depth of 60 m near Deep River. This reach is relatively calm (without rapids) except near Petawawa where there are numerous islands, faster currents, and shallow water. The majority of the study took place in a basin approximately 14 km long, characterized by sand and clay substrate with areas of rock rubble in faster flowing areas and relatively shallow depths with a maximum depth of 16.5 m (Figure 1).

Methods

Lake Sturgeon were captured in Allumette Lake late October 1998 with the use of 2.4 m trapnets set offshore near Desjardinsville, Quebec. Total length (to the nearest mm), fork length and weight (to the nearest 10 g) were obtained from Lake Sturgeon used in the study. Radio transmitters (model MBFT-6: Lotek Engineering Inc., Aurora, Ontario) were cylindrical with a whip antenna, measuring 11 mm (diameter) by 59 mm (length) and weighed 10.3 g (weight in water 4.6 g). The operating frequency was 149.140 to 149.820 MHz (Table 1) with a pulse rate of 29 beeps per minute. The expected life of these transmitters was 746 days.

TABLE 1. Attributes of Lake Sturgeon with radio transmitters implanted.

Sturgeon Number	Transmitter Frequency	Total length (cm)	Fork length (cm)	Weight (g)
140	149.140	84.7	76.0	2900
240	149.240	90.0	80.5	3500
320	149.320	98.0	87.5	4400
820	149.820	84.0	75.0	2675

Lake Sturgeon were anesthetized using tricaine methanesulfonate (MS222) and radio transmitters were surgically implanted. Radio transmitters and operating equipment were sterilized with isopropyl alcohol prior to use. A small incision was made in the abdomen wall, proximal to the midline ensuring the incision was not deep enough to damage internal organs. The incision exposed the peritoneal cavity and the transmitter was inserted into the peritoneum. The whip antenna was coiled inside of the peritoneum to prevent a source of irritation and infection that could be caused by a trailing antenna. The incision was closed with catgut suture material (sized 4-0). Each Lake Sturgeon was injected with Liquamycin (100 mg/mL of oxytetracycline hydrochloride) at a dose of 0.08 ml per kg and held in a recovery tank until fully revived. None displayed any effects from the procedure.

Tracking was conducted from both a boat and an airplane over a 2 ½ year period using a STR 100 Telemetry Receiver (Lotek Engineering Inc., Aurora, Ontario). Tracking was generally conducted once or twice a week during the spring and less frequently, once or twice a month, the remainder of the year. When tracking from a boat, a three-element folding antenna was used. Attempts were made to pinpoint the Lake Sturgeon, first by triangulation, then by closing in on the location in relation to the strength of the signal. Once a location was determined, UTM co-ordinates were obtained from a GPS unit. When using the plane to track, antennae were mounted on both wings. A switch box (ACU_1) was used to determine what side of the plane the signal originated. Locations were mapped as accurately as possible onto maps of the rivers and UTM co-ordinates later assigned to each point. A Walleye (*Sander vitreus*) telemetry project was conducted concurrently with this study (Haxton and Punt 2000*). Therefore, the entire length of the river reach was flown when tracking, including several reaches downstream.

UTM co-ordinates were entered onto an Access database along with the pertinent information about each tracking location (fish number, date, time). These co-ordinates were transferred into ArcView (Environmental Systems Research Institute, Redlands, California, USA) and a point coverage was made of all tracking locations. For tracking purposes, Lake Sturgeon were labeled by the frequency of the transmitter (i.e. the Lake Sturgeon with the radio transmitter of 149.820 was labeled Lake Sturgeon 820).

Distance traveled was determined by using the measure feature in ArcView. For analysis purposes, the year was divided into four seasons: Spawn (May – June); Summer (July – August); Fall (September – December); and Winter (January – April). An ANOVA was conducted on $\log_{10}$ transformed distance data to ascertain if there was a difference in mean movement between seasons. A minimum convex polygon home range was calculated for each Lake Sturgeon using the Animal Movement Analysis Extension (Hooge 2000*). In all cases, the home range extended onto land. Home ranges were calculated only for the river portion by tabulating the area where the home range and water polygons overlapped.

Depth of Lake Sturgeon occurrence was determined by overlaying their location onto a bathymetry map. The general depth of the area was used. It was assumed Lake Sturgeon were on bottom at time of tracking. An ANOVA was conducted to determine if there was a difference in depth utilized based on season.

Statistical analysis was conducted using SYSTAT 10.2 (SYSTAT Software Inc. Richmond, California, USA) with significance level determined at $P = 0.05$.

Results

Mean size of Lake Sturgeon in this study was 89.2 cm total length (Table 1). Radio tracking was found to be most effective and efficient from an airplane and subsequently was the primary means of tracking. Lake Sturgeon were tracked on 43 different occasions, for 110 observations (Figure 1). Three or more sturgeon were located on 48.8% of the trackings. The number of times each sturgeon was located was between 23 and 32 occasions (Table 2). All sturgeon were located in 2001, the last year of the study.

Lake Sturgeon displayed fidelity to the same basin that they were originally sampled, primarily concentrated offshore of Desjardinsville opposite Pembroke (Figure 1). There was some movement outside, or to the periphery, of the basin. Sturgeon 820 moved to the faster flowing water near the lighthouse off Île Leblanc from January through until early April 1999 but then returned to the basin by May. It later moved upstream to the Petawawa Islands for at least a week in July 1999. Sturgeon 140 was located in this vicinity of the lighthouse at the end of April 1999 and Sturgeon 240 was located there in September 1999. Sturgeon 320 moved into Hazley Bay, a small shallow Bay with depths less than 2.4 m, on two separate

FIGURE 1. Lower portion of Allumette Lake (Ottawa River) with Lake Sturgeon tracking locations identified.

occasions. And sturgeon 140 was located at the top of Lower Allumette Rapids in March of 1999 and 2001. Lake Sturgeon were not tracked within 52 km of the dam.

The average distance moved between trackings was 2.5 km. The maximum distance traveled between trackings was 10.6 km by Lake Sturgeon 820 between 13 July and 10 August. Average movement between seasons was not significantly different (ANOVA 3,101, $F = 0.718$, $P = 0.544$). Average home range for the four Lake Sturgeon was 1528 ha (Table 2).

Lake Sturgeon were generally found in shallow water; mean depth was 3.5 (2.1 S.D.) m. There was variation in mean depth of Lake Sturgeon between seasons (Figure 2); however, these differences were not significant ($ANOVA_{3,105}$, $F = 1.415$, $P = 0.242$). Lake Sturgeon were sometimes located in areas with water depths up to 12 m.

Discussion

In contrast to the findings of McKinley et al. (1998), Lake Sturgeon in the present study did not move extensively throughout the reach but displayed high fidelity to the one particular basin, sometimes leaving the basin but returning later. Homing or site fidelity by Lake Sturgeon has previously been described (Threader and Brousseau 1986; Fortin et al. 1993; Rusak and Mosindy 1997; Auer 1999; Caswell et al. 2004). This area of the river is characterized by a sandy, clay substrate, which should be productive for benthic invertebrates, the primary source of prey for sturgeon. Juvenile sturgeon will remain in areas where there is

TABLE 2. Average home range, average movement, number of times tracked and last date tracked for each Lake Sturgeon

Sturgeon number	Number of times tracked	Home range (ha)	Average movement (km)	Last date tracked
140	26	1645	2.5	25 May 2001
240	32	1066	1.5	25 May 2001
320	23	1348	2.6	25 May 2001
820	29	2054	3.2	7 November 2001

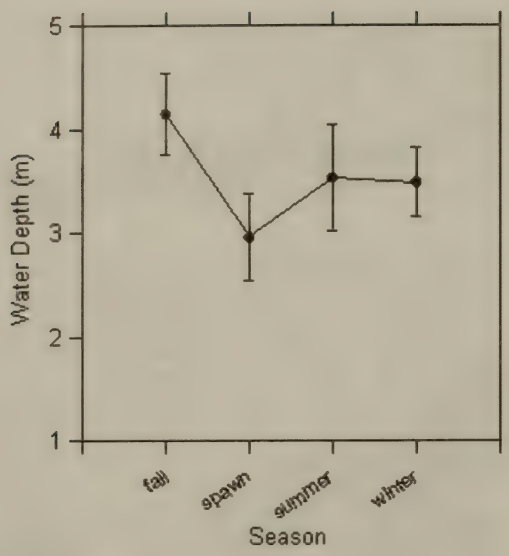


FIGURE 2. Mean depth of Lake Sturgeon by season (error bars in standard deviations).

moderate abundance of a prey species (Chiasson et al. 1997). Lake Sturgeon should not have been restricted upstream movement as Walleye in the concurrent study traveled up to 70 km to the base of the Rolphton Dam (Haxton and Punt 2000*).

Unfortunately, neither sex, stage of maturity nor age was assessed when implanting radio transmitters. Lake Sturgeon attains sexual maturity in lower Ottawa River reaches at 92 cm and 83 cm total length for females and males, respectively (Dubrueil and Cuerrier 1950), which would suggest that these sturgeon could have been mature. Recent studies on Lake Sturgeon maturity in this river reach, however, suggest that maturity is not attained until a total length of 115 cm (Haxton, unpublished data). Therefore, Lake Sturgeon used in this study were probably juveniles, at least at the time when radio transmitters were implanted. However, since sex and stage of maturity were not assessed, it is difficult to ascertain whether lack of movement to upper portions of the river reach was due to spawning periodicity (Roussow 1957), habitat requirements fulfilled within the basin, or prey abundance for juveniles (Chiasson et al. 1997).

Lake Sturgeon in this study were found in relatively shallow water. This is comparable to a 2 – 6 m preference by Lake Sturgeon in the Groundhog River in northern Ontario (Seyler 1997) and depths < 2.5 m in the Mattagami River (McKinley et al. 1998). Lake Sturgeon, however, were most frequently located in water depths > 6 m in Rainy Lake (Rusak and Mosindy 1997). Lake Sturgeon usually inhabit waters from 4 to 9 m (Houston 1987). The mean water depth utilized may have been skewed by the inability to locate all Lake Sturgeon on each tracking. Radio transmitter signal decreases as their depth increases. Generally, when radio transmitters are in depths greater than 9 m, the ability to detect a signal is low. While this study did locate Lake Sturgeon in depths of 12 m, I feel the reason we were not able to locate each sturgeon during each flight was because some were in deep water and the radio transmitter was weak. Therefore, the mean depths reported as preferred here may be low.

While there were some inherent problems with this project (i.e., Lake Sturgeon were not studied intensely enough to assess seasonal movement and habitat selection; the number of sturgeon tracked was small (n=4); and tracking was primarily geared around Walleye), this study did elucidate some details about the extent of sturgeon movement in a natural reach. Although movement by Lake Sturgeon in this study was limited, this did not appear to be due to the presence of dams as these were beyond the areas occupied.

Acknowledgments

Several key people that were instrumental in the completion of this study include: Gord Pearson, Pilot, Ontario Ministry of Natural Resources; Kirby Punt, Senior Fish and Wildlife Technician, Ontario Ministry of Natural Resources, Pembroke District; Pembroke Outdoors Sportman's Club (who spent many hours tracking Walleye and Lake Sturgeon); and several Pembroke District staff.

Documents Cited (marked * in text)

Haxton, T., and **K. Punt.** 2000. Walleye telemetry study to determine the spawning locations in Lac des Chats and Allumette Lake sections of the Ottawa River. Ontario Ministry of Natural Resources, Pembroke District, Pembroke, Ontario. Unpublished report.

Hooge, P. N. 2000. Animal Movement Analysis Arcview Extension. Alaska Biological Science Centre, Glacier Bay Field Station.

Literature Cited

Auer, N. A. 1996. Response of spawning Lake Sturgeon to changes in hydroelectric facility operation. Transactions of the American Fisheries Society 125: 66-77.

Auer, N. A. 1999. Population characteristics and movements of Lake Sturgeon in the Sturgeon River and Lake Superior. Journal of Great Lakes Research 25: 282-293.

Caswell, N. M., D. L. Peterson, B. A. Manny, and **G. W. Kennedy.** 2004. Spawning by lake sturgeon (*Acipenser fulvescens*) in the Detroit River. Journal of Applied Ichthyology 20: 1-6.

Chiasson, W. B., D. L. G. Noakes, and **F. W. H. Beamish.** 1997. Habitat, benthic prey, and distribution of juvenile Lake Sturgeon (*Acipenser fulvescens*) in northern Ontario rivers. Canadian Journal of Fisheries and Aquatic Science 54: 2866-2871.

D'Amours, J. S. Thibodeau, and **R. Fortin.** 2001. Comparison of Lake Sturgeon (*Acipenser fulvescens*), *Stizostedion* spp., *Catostomus* spp., *Moxostoma* spp., quillback (*Carpoides cyprinus*) and mooneye (*Hiodon tergisus*) larval drift in Des Prairies River, Quebec. Canadian Journal of Zoology 79: 1472-1489.

Dubreuil, R., and **J. P. Cuerrier.** 1950. Cycle du maturation des glands génitales chez l'esturgeon de lac (*Acipenser fulvescens*, Raf.). Institut de Biologie géneral et de Zoologie, Université de Montréal. 50 pages.

Dumont, P., R. Fortin, G. Desjardins, and **M. Bernard.** 1987. Biology and exploitation of Lake Sturgeon (*Acipenser fulvescens*) in the Quebec waters of the Saint-Laurent River. Pages 57-76 *in* Proceedings of a workshop on Lake Sturgeon (*Acipenser fulvescens*). *Edited by* C. H. Olver. Ontario Fisheries Technical Report Series Number 23.

Fortin, R., J-R. Mongeau, G. Desjardins, and **P. Dumont.** 1993. Movements and biological statistics of Lake Sturgeon (*Acipenser fulvescens*) populations from the St. Lawrence and Ottawa River system, Quebec. Canadian Journal of Zoololgy 71: 638-650.

Harkness, W. J. K., and **J. R. Dymond.** 1961. The lake sturgeon: the history of its fishery and problems of conservation. Ontario Department of Lands and Forests, Fish and Wildlife Branch, Toronto. 121 pages.

Haxton, T. J. 2002. An assessment of Lake Sturgeon (*Acipenser fulvescens*) in various reaches of the Ottawa River. Journal of Applied Ichthyology 18: 449-454.

Haxton, T., and **D. Chubbuck.** 2002. Review of the historical and existing natural environment and resource uses on the Ottawa River. Ontario Ministry of Natural Resources, Science and Information Branch, Southcentral Science and Information Section Technical Report #119. 76 pages.

Houston, J. J. 1987. Status of the Lake Sturgeon, *Acipenser fulvescens*, in Canada. Canadian Field-Naturalist 101: 171-185.

Kempinger, J. J. 1988. Spawning and early life history of Lake Sturgeon in the Lake Winnebago system, Wisconsin. American Fisheries Society Symposium 5: 111-122.

McKinley, S., G. Van Der Kraak, and **G. Power.** 1998. Seasonal migrations and reproductive patterns in the Lake Sturgeon, *Acipenser fulvescens*, in the vicinity of hydroelectric stations in northern Ontario. Environmental Biology of Fishes 51: 245-256.

Priegel, G. R., and **T. L. Wirth.** 1971. The lake sturgeon. Its life history, ecology and management. Wisconsin Department of Natural Resources, Madison, Wisconsin. Publication 270-277.

Roussow, G. 1957. Some considerations concerning sturgeon spawning periodicity. Journal of the Fisheries Research Board of Canada 14: 553-572.

Rusak, J. A., and **T. Mosindy.** 1997. Seasonal movements of Lake Sturgeon in Lake of the Woods and the Rainy River, Ontario. Canadian Journal of Zoology 74: 383-397.

Seyler, J. 1997. Adult lake sturgeon (*Acipenser fulvescens*) habitat use, Groundhog River. Ontario Ministry of Natural Resources, Northeast Science and Technology. Timmins, Ontario. Report TR-035. 20 pages.

Threader, R. W., and **C. S. Brousseau.** 1986. Biology and management of the lake sturgeon in the Moose River, Ontario. North American Journal of Fisheries Management 6: 383-390.

Tody, W. H. 1974. Whitefish, sturgeon, and the early commercial fishery. Pages 45-60 *in* Michigan Fisheries Centennial Report 1873 – 1973. Michigan Department of Natural Resources, Lansing, Michigan.

Williamson, D. F. 2003. Caviar and conservation: Status, management and trade of North American Sturgeon and Paddlefish. TRAFFIC North America. World Wildlife Fund, Washington, D.C.

Received 13 November 2001
Accepted 7 May 2004

An Aerial Survey Technique for the Forest-Dwelling Ecotype of Woodland Caribou, *Rangifer tarandus caribou*

RÉHAUME COURTOIS[1,2,5], ANDRÉ GINGRAS[3], CLAUDE DUSSAULT[4], LAURIER BRETON[1] and JEAN-PIERRE OUELLET[5]

[1]Société de la faune et des parcs du Québec, Direction de la recherche sur la faune, 675, René-Lévesque, Est, 11e étage, boîte 92, Québec, Québec G1R 5V7 Canada ; e-mail : rehaume.courtois@fapaq.gouv.qc.ca
[2]Université Laval, Département de foresterie et de géomatique, Cité Universitaire, Ste-Foy, Québec G1K 7P4 Canada
[3]Société de la faune et des parcs du Québec, Direction de l'aménagement de la faune, 818, boulevard Laure Sept-Îles, Québec G4R 1Y8 Canada
[4]Société de la faune et des parcs du Québec, Direction de l'aménagement de la faune, 3950 boulevard Harvey, 4e étage, Jonquière, Québec G7X 8L6 Canada
[5]Université du Québec à Rimouski, Département de biologie et des sciences de la santé, Centre d'études nordiques, 300, Allée des Ursulines, Rimouski, Québec G5L 3A1 Canada

Courtois, Réhaume, André Gingras, Claude Dussault, Laurier Breton, and Jean-Pierre Ouellet. 2003. An aerial survey technique for the forest-dwelling ecotype of Woodland Caribou, *Rangifer tarandus caribou*. Canadian Field-Naturalist 117(4): 546-554.

Accurate and precise population estimates for the forest-dwelling ecotype of Woodland Caribou (*Rangifer tarandus caribou*) are very difficult to obtain because these Caribou are found at very low densities and in small herds dispersed over large areas. In order to suggest a standardized method, data from aerial surveys conducted in 1991 and 1993 (12 000 km^2 blocks) were used to simulate various survey scenarios. Simulations showed that all the major groups of Caribou would have to be found and counted to obtain a confidence interval of ± 20% ($\alpha = 0.10$). We tested this technique in a survey carried out in winter 1999 in a 42 539 km^2 study site, opting for a total coverage carried out in two phases. In phase one, we used an airplane, flying north-south transects spaced 2.1 km apart so as to detect most Caribou track networks. In phase two, a helicopter was used to count and determine the sex and age classes (calves/adults) of Caribou found in phase one. Using 20 radio-collared Caribou, the visibility rate of Caribou groups (phase one) and that of Caribou within the groups (phase two) were estimated at 0.90 and 0.94 respectively for an overall rate of 0.85 (SE = 0.08; $\alpha = 0.10$). The corrected density was estimated at 1.6 Caribou per 100 km^2 with a 15% confidence interval ($\alpha = 0.10$). The survey cost approximately \$4/km^2, which is lower than that of two previous surveys (\$7/km^2). Two main factors contributed to diminish costs: (1) the use of long-range airplanes (5-7 hours flying range) in phase one to minimize travel between the airports and the study site, and (2) the use of helicopters only in phase two for counting and determining the age and sex of the Caribou.

Key Words: Woodland Caribou, *Rangifer tarandus caribou*, accuracy, aerial survey, bias, cost, density, forest-dwelling ecotype, simulation, visibility rate, Quebec.

Il est très difficile d'obtenir des estimations de population exactes et précises pour l'écotype forestier du Caribou des bois (*Rangifer tarandus caribou*) parce qu'on le retrouve en très faibles densités et qu'il est distribué en petites hardes réparties sur de vastes superficies. Les résultats de deux inventaires aériens réalisés en 1991 et 1993 (12 000 km^2) ont été utilisés pour simuler divers scénarios d'inventaire afin de suggérer une méthode standardisée. Les simulations ont montré qu'il fallait trouver et recenser tous les groupes principaux pour obtenir un intervalle de confiance de ± 20 % ($\alpha = 0,10$). Nous avons testé cette approche dans un site d'étude de 42 539 km^2 où nous avons opté pour un plan en deux phases. En phase un, l'avion a été utilisé pour couvrir totalement le site d'étude selon des virées équidistantes de 2,1 km afin de détecter la plupart des réseaux de pistes. L'hélicoptère fut utilisé en phase deux pour dénombrer et sexer les Caribous dans les réseaux de pistes détectés en phase un. D'après 20 Caribous munis de colliers émetteurs, le taux de visibilité global était de 0,85 (SE = 0,08; $\alpha = 0,10$), soit 0,90 en phase 1 et 0,94 en phase 2. La densité corrigée était de 1,6 Caribou par 100 km^2 avec une erreur relative de 15 % ($\alpha = 0,10$). L'inventaire a coûté 4 \$/km^2, ce qui est inférieur aux montants investis lors des inventaires antérieurs (7 \$/km^2). La diminution des coûts est attribuable à deux facteurs principaux : (1) l'utilisation d'avions à grand rayon d'action (5-7 heures d'autonomie) pour minimiser les déplacements en phase un; (2) l'emploi d'hélicoptères exclusivement pour le dénombrement et le sexage des caribous.

Mots clés : Caribou des bois, *Rangifer tarandus caribou*, biais, coût, densité, écotype forestier, inventaire aérien, précision, taux de visibilité, simulation, Québec.

The forest-dwelling ecotype of Woodland Caribou (*Rangifer tarandus caribou*) is found at very low densities and is distributed in small herds dispersed over large areas (Courtois et al. 2001). According to systematic surveys carried out during the 1960s and 1970s, the southern limit of distribution is about the 49th parallel in eastern, and the 50th parallel in western Quebec (Brassard 1972*). These surveys revealed the presence of six large forest-dwelling herds, each comprising from a few hundred to several thousand animals. Outside these herds, a number of scattered smaller groups were also found, composed of 75 or fewer Caribou. Farther south, Woodland Caribou were limited to two small, isolated herds totalling less than 300 individuals.

Survey techniques for the forest-dwelling ecotype of Caribou have varied considerably over the years depending on the groups being targeted. Large herds were inventoried on traditional wintering areas by means of equidistant transects (Le Hénaff 1976a*,b*; Folinsbee 1979), whereas, the smaller herds in southern Quebec were usually surveyed using total coverage after delimiting the area utilized by means of telemetry (Cantin 1991*; Paré and Brassard 1994*; Desrosiers and Faubert 1995*). No recent estimates are available for the entire forest-dwelling Caribou population. A few estimates have been attempted using random designs, but they were imprecise and probably biased (Joly and Brassard 1980*). Sampling is made difficult by very low densities, usually less than 1.5 Caribou per 100 km^2 and by the aggregation of individuals in small groups with clumped distribution (Crête 1991*). In addition, Caribou living in forest habitats are difficult to locate and their visibility has never been estimated in eastern Canada. Some attempts have been made in British Columbia (D. Heard, personal communication, September 2001), but the survey conditions (e.g., snow cover, tree height, canopy cover, group size, etc.) likely differ among regions. Given these difficulties, it has been proposed to monitor only population trends (1) in a few control areas by total coverage (Gingras and Malouin 1993*; Bourbonnais et al. 1997*) or (2) in hunting zones, based on observations made during Moose, *Alces alces*, surveys (Courtois et al. 1996*). The first approach proved to be effective in estimating the density in relatively small control sites, but turned out to be expensive and the results could not be extrapolated to the entire range (Courtois et al. 1996*). The second approach was inexpensive, but did not allow delimitation of the exact location of each herd, thereby limiting its usefulness for forest management purposes.

Given the lack of an accurate, unbiased and inexpensive survey technique, the present-day locations, abundance and dynamics of forest-dwelling populations are not known (Crête et al. 1990*). This lack of knowledge is of concern, given the precarious situation of forest-dwelling Caribou throughout their range in North America (Mallory and Hillis 1998). Furthermore, for about the last 20 years, there has been a significant northern expansion of forestry operations. As a result, adequate management of forest-dwelling Caribou and their habitat requires a better knowledge of the locations of herds and the population trends. By using the data from two previous surveys, we simulated various sampling scenarios in order to identify a technique that could be applied to large areas. This technique was subsequently tested in a 42 539 km^2 study site to verify its applicability and to evaluate costs. The feasibility of surveying Woodland Caribou populations over their entire distribution range in Québec is discussed.

Methods

Thirty survey reports prepared between 1953 and 1997 were used to determine the most suitable periods for surveying forest-dwelling Caribou, as well as the composition of survey teams, types of aircraft and the flying altitude and speed. Data used in the simulations came from two aerial surveys carried out in 1991 and 1993 in two 12 000 km^2 blocks (≈69.0° W, 50.0° N and ≈63.0° W, 50.5° N; Gingras and Malouin 1993*; Bourbonnais et al. 1997*). These sites were first totally flown over by airplane in 1991, using north-south transects, and by helicopter in 1992, using transects spaced 10 km and 3 km, respectively. The sites had been previously divided into plots of 200 km^2 (1991) or 100 km^2 (1993), and flights allowed the study sites to be classified into two strata according to the presence or absence of Caribou tracks. A sub-sample of plots was then flown over by helicopter using equidistant north-south transects spaced 1 km apart. The track networks were then flown over at low altitude (100 m) in order to locate, count and sex individual Caribou. Five plots in each stratum were randomly chosen and surveyed at the beginning of the survey to calculate the Neyman optimal allocation (Snedecor and Cochran 1971), which was thereafter recalculated daily to allocate other plots until a confidence interval (CI) of 25% ($\alpha = 0.10$) or a sampling rate of 50% was obtained.

Assuming that these surveys constituted representative pre-tests, we simulated various sampling scenarios in a large, fictitious study site (36 000 km^2) constructed by randomly selecting sample plots from those flown over in 1991 and 1993. The simulations were set up to completely cover the high-density stratum, since the optimal allocation had suggested surveying all the plots in this stratum during the pre-tests. For the low-density stratum, 50 sampling scenarios were simulated by selecting between two and 100 sample plots. In each case, 100 simulations were carried out. Plots of 100 and 200 km^2 were tested, but the results were similar. Thus, only those results obtained with the 100 km^2 plots were reported.

Between 20 February and 28 March 1999, we surveyed Caribou in a 42 539 km^2 study site (≈ 66-71° W and 49-51° N), which included the area covered in 1991. We used a two-phase survey plan. In phase one, two airplanes (Navajo 350), each with a four-member team (pilot, navigator-observer, two observers), flew over the study site using equidistant transects spaced 2.1 km apart (1.75 minutes of longitude) at a speed of 200 km/h and an average altitude of 200 m. The study site had been divided into 40 km blocks along a north-south axis in order to limit the length of the transects and to reduce the fatigue of the observers. The territory to be covered was allocated randomly each day between the two teams. Observations (tracks of Caribou, Moose and unidentified cervids) were noted on 1:50 000 topographic maps and their central point was

positioned using GPS units that were used for navigation. As required, information (e.g., maps, positions of track networks) was exchanged between teams by means of fax and electronic mail.

In phase two, the track networks of Caribou and unidentified cervids were surveyed by helicopters (Bell 206B or Astar 350A) with a three-member team (pilot, navigator-observer, observer) in order to count and classify Caribou (males and females, adults and calves) along the track networks, based on the presence of a vulval patch, and antler and body size. Phase two was usually carried out the day after the phase one survey. During the helicopter counts, the team also noted the presence of radio-collared animals. These Caribou, which numbered 20 in total, were independently radio-located at the middle and at the end of the survey, in order to identify animals that were missed by the observers and to estimate the visibility rate of the Caribou in accordance with the method of Crête et al. (1986: 759). These Caribou had been collared the previous year to ensure their dispersal over the study site. The survey teams were not aware of the locations of marked Caribou at the time of the survey.

Results

The 30 consulted publications covered 83 aerial surveys of Caribou. Techniques used since the 1950s have varied considerably (Table 1). The most frequently used sampling plan was an inventory of continuous strips spaced systematically within the study areas (11 publications; 25 surveys). Surveys by sample plot (eight publications; 16 surveys) or flying over sites very likely to contain Caribou (seven publications; 38 surveys) were also frequent, the latter technique being used for smaller study areas or when high-density sites had been identified by means of telemetry. Complete coverage or mixed sampling plans were reported in four publications (four surveys). A helicopter (10 publications; 35 surveys) or an airplane (10 publications; 26 surveys) was used more often than an airplane and a helicopter simultaneously (five publications; 11 surveys), while the type of aircraft was not specified in four publications s (11 surveys). The use of airplanes alone was especially frequent in the oldest surveys. Spacing between the flight lines varied between two and 40 km, the widest spacing being used to stratify the study area before counting Caribou. Flight altitude usually varied between 150 and 250 m and speed was around 150 to 200 km/h. In open habitats, surveys were usually conducted in fall (mid-September to mid-October) or in late winter (mid-February to late March), whereas only the latter period was used in forested areas.

Surveys carried out in 1991 and 1993 produced results with apparent satisfactory precision, the reported CIs being 20.1% and 15.6% ($\alpha = 0.10$), respectively (Table 2). However, the visibility rate had not been estimated, with the result that the population estimates and their variance were likely underestimated since a part of the variation among the sample unit counts was due to visibility bias rather than actual differences in the number of animals present. The low-density stratum contained 18 and 21% of the Caribou. In 1991, the majority (25 out of 29) of groups located during the survey of the plots by helicopter, using transects spaced 1 km apart, had been detected by airplane during the stratification flight at every 10 km. The area of Caribou track networks averaged 3.1 km^2 ± 2.8 (12) (mean ± standard error [n]) in 1991 and 0.78 km^2 ± 0.3 (12) in 1993.

Variance among plots in the high-density stratum was very high (273.4 and 114.5 in 1991 and 1993, respectively; coefficient of variation [CV]: 129% and 128%), with the result that the Neyman optimal allocation had suggested a complete census of this stratum in both surveys. Most of the variability among plots was due to the heterogeneous distribution of Caribou within the study site, as well as highly variable group sizes (0-49 Caribou per plot in each year). The variance in the low-density stratum was also high given the low numbers of Caribou in these plots (S^2 = 5.4 and 0.9; CV = 383% and 427%). Most of them were empty, but some contained up to 10 Caribou because some track networks had been overlooked during stratification. This meant the sampling of a large number of plots without Caribou was needed to reduce the variance in this stratum.

For a study site of 36 000 km^2, the simulations showed that an average CI of 20% (α = 0.10) could be obtained by a complete survey of the high-density stratum, the equivalent of 33 of the 100 km^2 plots and 48 of the 327 plots in the low-density stratum (Figure 1a). However with this sampling effort, nearly 60% of the simulations had a CI higher than the desired threshold of 20% (Figure 1b). The mean of 100 simulations produced estimates close to the exact value. The mean difference varied between -2.2 to 6.0% depending on the simulation. In absolute value, the mean error of the estimate diminished with the number of plots surveyed in the low density stratum (Figure 1c). However, it would have been necessary to survey about 80 plots in that stratum to obtain a CI lower than 20% in about 90% of the surveys and with a sampling error < 10% (Figure 1d). Consequently, it appeared to be cheaper to fly at a sufficient intensity in phase 1 to find most of the track networks and then to count all of the Caribou there. In such a survey, the only source of variance would be that of the visibility rate, which could be estimated by means of radio-collared animals.

A preliminary cost estimate was carried out for three sampling designs: (1) stratified random sampling technique (SR) using the airplane and the helicopter (scenario used in 1991); (2) SR using the helicopter only (scenario in 1993); and (3) total coverage of the site by airplane with transects spaced 2.1 km, followed by a helicopter count in the track networks detected by

TABLE 1. Summary of techniques used in 83 Caribou aerial surveys (30 publications) conducted between 1953 and 1997 in Quebec and in other North American jurisdictions.

Author(s)	Area (km^2)	*n*	Method	Aircraft [a]	Transects spacing (km) phase 1 [b]	phase 2 [c]	Altitude (m)	Speed (km/h)	Plot size (km^2)	Period
Audet (1979)*	171 140	1	TR	H	10-40	-d	100-250	180	–	February
Anonymous (1968)*	92 700	1	TR	A	16	–	250-300	–	–	–
Anonymous (1979)*	87 000	1	TR	A+H	5	–	150-350			15 February-7 March
Anonymous (1988)*	122 000	1	TR	A	10-20	–	120	140-160	–	18 March -7 April
Anonymous (1992)*	146 760	1	ST	A+H	–	0.5	150	120	60	Mid-January/Early March
Banville (1998)*	1500	15	PS	A, H, A+H	–	1	100	160	–	February-March
Barnard (1983)*	48 000	1	SR	H	–	0.5	100	160	60	Mid-February
Bergerud (1963)	–	6	TR	A	8-32	0.8-32	150-300	130-160	–	Late February-Early March
Bergerud (1985)	1878	1	TR	H	2-5	–	–	–	–	January-February
Bergerud and Elliot (1986)	–	1	PS	–	–	–	–	–	–	Late Sept. -Mid-October
Boertje et al. (1996)	17 000	1	CC	–	–	–	–	–	–	–
Bourbonnais et al. (1997)*	12 000	1	ST	H	3.5	1	200	150-200	200	1-15 March
Brassard (1967)*	25 700	1	TR	A	16	–	240-300	–	–	Late February-Early March
Brassard (1972)*	29 135-250 250	7	TR, SR, CC	A	16	450-600	240-300		–	–
Brassard (1982)*	> 250 000	1	SR	A	–	–	–	–	–	January-February
Brassard and Brault (1997)*	5000	11	PS	H, A+H	–	–	300	–	–	Late March
Couturier et al. (1996)	49 000	1	TR	A+H	13	–	40-60	180	–	Mid-June
Cumming et al. (1996)	6500	4	TR, CC	–	3	–	300	–	–	Mid-late February
Desrosiers and Faubert (1995)*	109	1	PS	H	–	–	100	100	–	October
Edmonds (1988)	16 000	6	PS	H	–	–	75-100	–	–	Mid-late winter
Farnell et al. (1996)	7400/ 9600	4	ST	–	–	–	–	–	–	Rut or late winter
Folinsbee (1975)*	–	1	TR	A	–	5	125	–	–	29-30 March
Gingras and Malouin (1993)*	12 000	1	ST	A+H	10	1	200	200	200	26 February-23 March
Heard and Ouellet (1994)	5600 - 34 000	5	SR	A, H, A+H	4.3	–	120	≈ 185	–	November/March/late June
Joly and Brassard (1980)*	82 000	1	ST	A+H	–	0.5	–	–	60	–
Maltais (1997)*	3200	1	CC	H	2	2	200-400	150	–	27-31 January
Moisan (1957)	–	1	PS	A	–	–	150-300	160-200	–	November
Pichette and Beauchemin (1973)*	624 000	1	TR	A	16-64	–	300-360	–	–	30 January-20 February
Seip (1992)	5000	4	PS	H	–	–	–	–	–	Late March
Stuart-Smith et al. (1997)	20 000	1	SR	–	–	–	–	–	84	–

[a] *n*: n surveys considered; TR: strip census, SR: simple random; ST: stratified random; PS: potential sites; CC: complete coverage; A: airplane, H: helicopter.
[b] Aerial survey for locating track networks to either delimit areas occupied by the herds to be systematically surveyed or to stratify the area.
[c] Counting and sexing Caribou.
[d] Does not apply or value not reported.

TABLE 2. Results of two aerial surveys of Caribou conducted in 1991 and 1993 in two 12 000 km^2 study blocks on the North Shore of the St. Lawrence River, Quebec.

Stratum	Caribou seen / 100 km^2	Population estimate	Standard Error	CI (%)[a]	f[b]
1991 SURVEY					
High-density	6.1	141	0.0	0.0	1.00
Low-density	0.3	31	20.4	114.1	0.39
Total	1.4	172	20.4	20.1	0.50
1993 SURVEY					
High-density	8.4	92	0.0	0.0	1.00
Low-density	0.2	24	10.9	74.5	0.45
Total	1.0	116	10.9	15.6	0.50

[a] Confidence interval expressed in percentage of the estimated population ($\alpha = 0.10$).
[b] Sampling rate (number of plots flown / total number of plots).

the plane (Table 3). The third scenario appeared 23-35% less costly because it did not require a stratification flight and involved less travel between airports and the study site as well as between plots. This scenario also simplified the logistics of the survey and allowed for censuses of Moose and Wolf, *Canis lupus*, tracks.

In the 42 539 km^2 study site of 1999, this sampling strategy allowed us to locate 230 Caribou track networks varying in size from 0.06 to 9.52 km^2 (0.53 ± 0.06), and including between 0 and 64 Caribou (2.39 ± 0.42). The track networks were concentrated in three main sectors (Figure 2). The helicopter crew counted 572 Caribou. Eighteen of the 20 radio-collared Caribou (90%) were in the track networks identified in the airplane survey (phase one) and of these, 17 (94%) were observed during phase two using a helicopter. The visibility rate was estimated at 0.90 (SE = 0.067) in phase one, and 0.94 (0.056) in phase two, for an overall rate of 0.85 (0.081). The total population corrected for the visibility bias was estimated at 673 ± 100 Caribou (CI = 15%; $\alpha = 0.10$). The corrected density was 1.6 Caribou/100 km^2 ± 15% and there were 60.6 ± 4.5 males/100 females and 16.0% ± 1.4% calves in the population.

The survey cost of $160 100 includes the flight time needed to estimate the visibility rate. This figure is about $17,000 less than the estimate made during the planning of the survey (Table 3). It required 38% of the budget to fly over the study site, while 13% was used for airplane travel from and to the airports. The helicopter count represented 13% of the budget, while 17% was used for helicopter travel. The rest of the budget (19%) was used for survey crew lodging and various expenses.

Discussion

Aerial surveys carried out over the last 50 years illustrate the gregarious behaviour of Caribou, since groups of several dozen to a few thousand individuals have been observed within relatively small areas. Survey techniques have attempted to take advantage of this behaviour. For large northern herds, censuses were generally conducted during calving (Couturier et al. 1996) or post-calving aggregations (Rivest et al. 1994) when animals are concentrated into relatively small open areas making them easier to count.

However, no reliable method exists for Woodland Caribou living in forested habitats. Previous surveys were carried out in winter to take advantage of higher visibility for these animals and to facilitate their detection by means of tracks in the snow. However, the low densities encountered, and the aggregation into groups of variable size led to imprecise estimates. For example, Joly and Brassard (1980*) surveyed Moose and Caribou in 30 60-km^2 sample plots in an 82 000 km^2 study site south of James Bay (≈77.0° W, 50.5° N). They estimated the Moose population with an acceptable level of precision (CI = 25%, $\alpha = 0.10$) by utilizing the distribution of track networks that followed a Poisson distribution. However, not enough Caribou track networks were detected to allow the same technique to be applied to this species. In the early 1990s, 194 60-km^2 plots were surveyed in a 146 760 km^2 study site located east of James Bay (Anonymous 1992*). Even such a large sampling effort led to a very high CI (14 Caribou/100 km^2 ± 64%, $\alpha = 0.10$). During this survey, two high concentration areas were surveyed using transects spaced 10 km apart. In these smaller areas (≈ 26 000 km^2), density was estimated at 450 Caribou/100 km^2 with a 42% CI.

Previous surveys and our simulations showed that the main Caribou groups must be located and counted in order to reduce the variance in forest-dwelling Caribou surveys. Even in high concentration areas, previous survey techniques usually led to very high variances and significant biases/underestimations due to the gregarious behaviour of forest-dwelling Caribou and because some groups were missed during stratification. According to Bergerud (1963), snow depth may be the main factor influencing the distribution and size of groups, as Caribou become more concentrated in

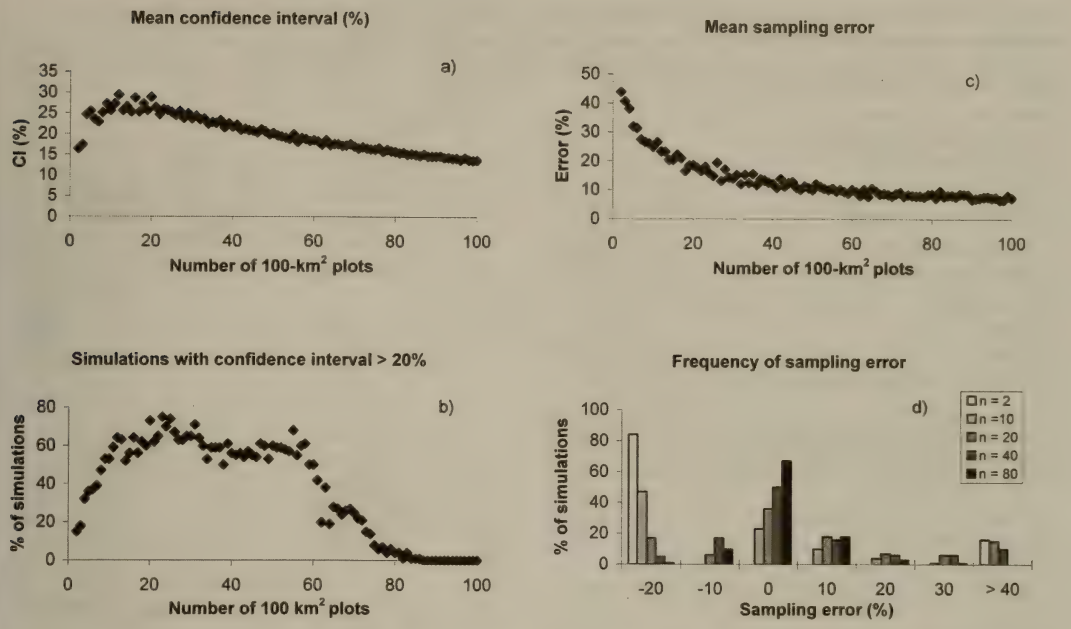


FIGURE 1. Influence of the number of plots surveyed in the low-density stratum (no Caribou track network detected during the stratification flight) on the precision of Caribou aerial surveys in forested habitats. Each point on the curve represents 100 simulations; (a) confidence interval (CI) of the estimated population ($\alpha = 0.10$); (b) % of simulations producing CIs > 20% ($\alpha = 0.10$); (c) mean sampling error, in absolute value (100 * [| estimated value – exact value |] / exact value), obtained according to the number of plots surveyed; (d) % of simulations per sampling error class and according to the number of plots surveyed.

deeper snow that limits availability of feeding sites. This author suggested covering the entire study site by plane to locate the main concentration areas (≥ 232 Caribou/100 km^2). He then advised surveying these areas in a width-wise direction using strips covering ≥ 33% of their surface area. In closed habitats, strips should cover about 400 m on each side of the airplane at 150 m altitude. Strip width and altitude could be doubled in open habitats. In forested sites, surveys should be carried out when the snow is deepest. The Caribou are thus more concentrated and less inclined to frequent closed habitats in search of arboreal lichens. Bergerud (1963) estimated that this method would underestimate numbers by about 20% (extremes: 10-40%) in high concentration areas.

We suggest that such a methodology, designed for areas used by large herds of forest-dwelling Caribou, should be applied to the entire study area when densities are very low. In that case, groups of Caribou are small and they occupy relatively small track networks (< 3 km^2). During the 1991 and 1993 surveys, respectively, 18 and 21% of the Caribou surveyed were in track networks that were not observed during the stratification flight using transects spaced three to 10 km apart (Gingras and Malouin 1993*; Bourbonnais et al. 1997*). In the site surveyed in 1999, the track networks of the three main herds would have probably been detected by a stratification flight made using transects spaced 10 km apart. However, many isolated track networks would have been missed. These included between 160 and 170 Caribou in total or nearly 30% of the number surveyed.

With transects spaced 2.1 km apart, the visibility rate was estimated to be 85% and a 15% CI ($\alpha = 0.10$) was obtained, a precision higher than the acceptable threshold (20%, $\alpha = 0.10$) suggested for cervid inventories in North America (Gasaway and Dubois 1987). However, the visibility rate must be considered a first approximation because it was established using a relatively limited number of Caribou and because males were under-represented (3 individuals in 20). Surveys should be conducted between mid-February and mid-March, because the Caribou seem more inclined to frequent open habitats during that period. In addition, the observation conditions are better (e.g., sunny, longer and warmer days) than in January.

Based on the 1999 inventory, such a survey cost \$4/km^2, which was less than the amount invested for stratified random sampling in areas one third the size of our study site (\$7/km^2; Gingras and Malouin 1993*; Bourbonnais et al. 1997*). Reduction in cost during the 1999 survey was attributed to two main factors: (1) the

TABLE 3. Estimated cost for the aerial survey of Caribou in a 42 539 km^2 block according to three sampling scenarios.

	Flight time (h)	Aircraft	Cost (× $1000)
Stratified random sampling (airplane and helicopter: 1991 scenario)			
Stratification (10 km interval)	24.8	Airplane[a]	9.9
Stratification - travel	28.3	Airplane	11.3
Survey of plots (1 km interval)	131.0	Airplane	52.4
Travel for survey flights	156.9	Airplane	62.8
Counting and sexing	53.1	Helicopter[b]	37.2
Travel for sexing	28.3	Helicopter	19.8
Lodging	–	–	40.6
Other	–	–	3.9
Total			237.9
Stratified random sampling (helicopter only: 1993 scenario)			
Stratification (3.5 km interval)	75.8	Helicopter	53.1
Survey of plots at 1 km intervals	129.3	Helicopter	90.5
Counting and sexing	40.7	Helicopter	28.5
Travel	83.6	Helicopter	58.5
Sling of fuel	12.4	Helicopter	8.7
Lodging	–	–	40.6
Other	–	–	3.9
Total			283.7
Total coverage (airplane and helicopter: 1999 scenario)			
Survey (2.1 km intervals)	100.0	Airplane	40.0
Airplane travel	30.0	Airplane	12.0
Counting and sexing	40.7	Helicopter	28.5
Helicopter travel	83.6	Helicopter	58.5
Lodging	–	–	40.6
Other	–	–	3.9
Total			183.5

[a] Cost estimated at $400/h

[b] Cost estimated at $700/h

use of long-range airplanes (5-7 hour flight range) to minimize the travel during phase one, and (2) restricted use of helicopters, which are more costly, only for counting and sexing Caribou.

Relevance and Costs of a Forest-Dwelling Caribou Aerial Survey Program

There are different alternatives to monitor trends of forest-dwelling Caribou populations. For example, changes in distribution (Cumming and Beange 1993), rates of recruitment (Bergerud and Elliot 1986), or survival (Rettie and Messier 1998) had previously been used. However, each method has its own limitations and it would be difficult and costly to use these alternative methods because forest-dwelling Caribou live in low density spread over large areas. Aerial surveys are probably the best source of information to provide distribution, abundance and recruitment estimates simultaneously. This alternative also allows delimiting the area occupied by each herd, which is essential for habitat management purposes.

Information collected over the last 40 years in Quebec shows that the distribution of forest-dwelling Caribou is limited to the boreal forest (Courtois et al. 2003). More specifically, they are principally found in the eastern part of the bioclimatic zone of spruce/moss forest, where the fire cycle is very long. About 90% of observations were reported within ≈ 234 500 km^2, which could be considered as the actual zone of continuous distribution of forest-dwelling Caribou in the province. Using the 1999 survey method, a survey of this area would cost nearly one million dollars. However, about $257 700 would be sufficient to survey the zones of intensive use (≈ 64 400 km^2), where about 70% of Caribou observations have been made (Courtois et al. 2003). The rest of the area frequented by Caribou could be surveyed in an ad hoc fashion, for example, during the planning phase of forest operations. The surveys could be carried out as part of a five-year program in which Moose and Wolf tracks would also be located and the habitats used by Caribou and these two species would be studied.

Isolated herds south of the 49th parallel are already the focus of an aerial survey program. With regards to the forest-dwelling herds in northern Quebec it does

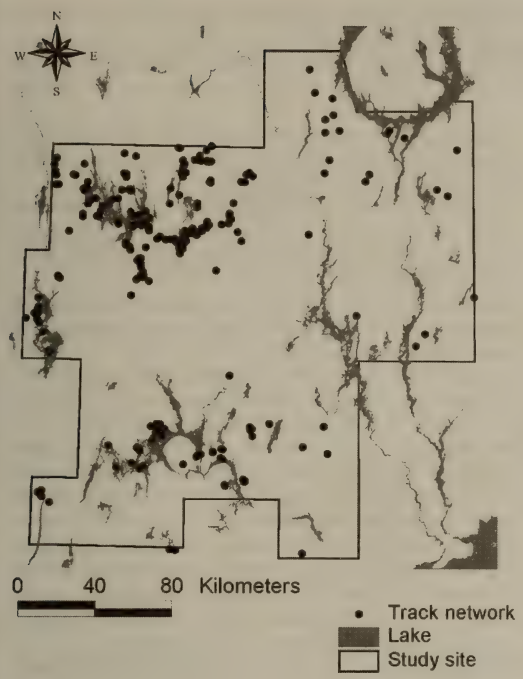


FIGURE 2. Locations of Caribou track networks during the survey of a 42 539 km^2 study block on the Quebec North Shore, Canada, February and March 1999.

not seem appropriate to survey them because they co-occur with migratory barren-ground Caribou in winter (Paré 1987; Brown et al. 1986; Anonymous 1992*), which prevents unbiased estimates from being obtained.

Acknowledgments

The authors acknowledge the contribution of the personnel of the Service de l'aménagement et de l'exploitation de la faune at Sept-Îles and Jonquière who provided the aerial surveys. We are particularly indebted to Pierre Drapeau, Christian Dussault, Douglas Heard, François Potvin, James Schaefer and two anonymous referees who reviewed draft versions of this paper and suggested many improvements. This project was financed by the Société de la faune et des parcs du Québec, the Ministère des Ressources naturelles du Québec, the Association des manufacturiers de bois de sciage du Québec, the Fondation de la faune du Québec, Abitibi-Consolidated Inc. and Kruger (Scierie-Manic).

Documents Cited (marked * in text)

Anonymous. 1968. Inventaire aérien des ongulés sauvages, section située dans le nord de l'Abitibi (janvier 1968). Service de la Faune. Québec, Québec. 7 pages.

Anonymous. 1979. Inventaire aérien des ongulés de la Côte-Nord, 1979. Hydro-Québec, Direction de l'Environnement. Montréal, Québec. 5 pages + appendix.

Anonymous. 1988. Late winter distribution of caribou and moose in southern Labrador and the Québec North Shore. Renewable Resources Consulting Services Ltd., Sidney, B.C. and S. Fudge and Associates Limited, St. John's, Newfoundland. 27 pages.

Anonymous. 1992. Complexe Nottaway-Broadback-Rupert: Les mammifères – volume 3 – Abondance et habitat du caribou (*Rangifer tarandus*). Hydro-Québec, Vice-présidence Environnement, Montréal, Québec. 55 pages + appendix.

Audet, R. 1979. Inventaire aérien de l'ensemble du bassin versant de la moyenne et de la basse Côte-Nord. Hydro-Québec, Direction de l'Environnement. Montréal, Québec. 42 pages.

Banville, D. 1998. Plan de gestion du caribou de Charlevoix. Ministère de l'Environnement et de la Faune. Charlesbourg, Québec. 26 pages.

Barnard, F. 1983. Rapport de l'inventaire aérien des ongulés de la basse Côte-Nord en février 1983. Ministère du Loisir, de la Chasse et de la Pêche. Sept-Îles, Québec. 11 pages.

Bourbonnais, N., A. Gingras, and **B. Rochette.** 1997. Inventaire aérien du caribou dans une portion de la zone de chasse 19 sud (partie est) en mars 1993. Ministère de l'Environnement et de la Faune. Sept-Îles, Québec. 11 pages.

Brassard, J.-M. 1967. Inventaire aérien des ongulés sauvages de la Côte-Nord et identification des aires d'hivernement en fonction des formes du relief et de la végétation. Service de la Faune. Québec, Québec. 15 pages.

Brassard, J.-M. 1972. Inventaire aérien du gros gibier. Ministère du Tourisme, de la Chasse et de la Pêche. Québec, Québec. 39 pages.

Brassard, J.-M. 1982. Inventaire aérien du caribou des territoires situés sur les versants de la Côte-Nord du Saint-Laurent. Ministère du Loisir, de la Chasse et de la Pêche. Québec, Québec. 13 pages.

Brassard, C., and **M. Brault.** 1997. État de la situation du caribou des bois (*Rangifer tarandus caribou*) de la Côte-Nord du Saint Laurent. Ministère de l'Environnement et de la Faune, Baie-Comeau, Québec. 62 pages.

Cantin, M. 1991. Tendances démographiques de la population de caribous (*Rangifer tarandus*) des Grands-Jardins. Ministère du Loisir, de la Chasse et de la Pêche. Charlesbourg, Québec. 26 pages.

Courtois, R., F. Potvin, S. Couturier, and **A. Gingras.** 1996. Révision des programmes d'inventaires aériens des grands cervidés. Ministère de l'Environnement et de la Faune. Québec, Québec. 49 pages.

Crête, M. 1991. Mise au point de la technique d'inventaire du caribou dans la taïga. Ministère du Loisir, de la Chasse et de la Pêche. Québec, Québec. 20 pages.

Crête, M., R. Nault, and **H. Laflamme.** 1990. Caribou. Ministère du Loisir, de la Chasse et de la Pêche. Québec, Québec. 73 pages.

Desrosiers, A., and **R. Faubert.** 1995. Méthode d'inventaire aérien pour déterminer la composition automnale de la population de caribous du parc de la Gaspésie et synthèse des résultats obtenus entre 1953 et 1994. Ministère du Loisir, de la Chasse et de la Pêche. Québec, Québec. 22 pages.

Folinsbee, J. D. 1975. An aerial survey of the Lac Joseph Caribou Herd, March 1975. Newfoundland Wildlife Service, St. John's, Newfoundland. 14 pages.

Gingras, A., and **B. Malouin**. 1993. Inventaire aérien du caribou dans la zone de chasse 19 sud (partie ouest) en mars 1991. Ministère du Loisir, de la Chasse et de la Pêche. Sept-Îles, Québec. 26 pages.

Joly, R., and **J.-M. Brassard.** 1980. Inventaire aérien des ongulés d'une portion sud du territoire de la municipalité de la Baie James. Ministère du Loisir, de la Chasse et de la Pêche. Québec, Québec. Report DGF 16: 116-136.

Le Hénaff, D. 1976a. Vérification des principales aires du caribou (*Rangifer tarandus*) dans le secteur de Waco (basse Côte-Nord) et au Nouveau Québec, avril 1976. Ministère du Tourisme, de la Chasse et de la Pêche. Québec, Québec. 31 pages.

Le Hénaff, D. 1976b. Inventaire aérien du secteur Natashquan à Blanc-Sablon. Ministère du Tourisme, de la Chasse et de la Pêche. Québec, Québec. 7 pages.

Maltais, J. 1997. Inventaire de reconnaissance (aire commune 24-1): caribous des bois (*Rangifer tarandus*) de la région des lacs Péribonca et Manouane. Abondance et besoins de l'espèce par rapport à l'exploitation forestière. Stone-Consolidated Inc., Division Saguenay. Chicoutimi, Québec. 39 pages + appendix.

Paré, M., and **C. Brassard.** 1994. Écologie et plan de protection de la population de caribous de Val-d'Or. Ministère de l'Environnement et de la Faune. Rouyn-Noranda, Québec. 56 pages.

Pichette, C., and **P. Beauchemin.** 1973. Inventaire aérien du caribou. Ministère du Tourisme, de la Chasse et de la Pêche. Québec, Québec. 11 pages.

Literature Cited

Bergerud, A. T. 1963. Aerial census of caribou. Journal of Wildlife Management 27: 438-449.

Bergerud, A. T. 1985. Antipredator strategies of caribou: dispersion along shorelines. Canadian Journal of Zoology 63: 1324-1329.

Bergerud, A. T., and **J. P Elliot.** 1986. Dynamics of caribou and wolves in Northern British Columbia. Canadian Journal of Zoology 64: 1515-1529.

Boertje, R. D., P. Valkenburg, and **M. E. McNay.** 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. Journal of Wildlife Management 60: 474-489.

Brown, W., J. Huot, P. Lamothe, M. Paré, G. St-Martin, and **J. B. Theberge.** 1986. The distribution and movement patterns of four woodland caribou herds in Quebec and Labrador. Rangifer, Special Issue 1: 43-49.

Courtois, R., J.-P. Ouellet, A. Gingras, C. Dussault, and **D. Banville.** 2001. La situation du caribou forestier au Québec. Naturaliste Canadien 128: 53-63.

Courtois, R., J.-P. Ouellet, A. Gingras, C. Dussault, L. Breton, and **J. Maltais.** 2003. Historical changes and current distribution of Caribou, *Rangifer tarandus*, in Quebec. Canadian Field-Naturalist 117: 399-414.

Couturier, S., R. Courtois, H. Crépeau, L.-P. Rivest, and **S. Luttich.** 1996. The June 1993 photocensus of the Rivière George caribou herd and comparison with an independent census. Rangifer, Special Issue 9: 283-296.

Crête, M., L.-P. Rivest, H. Jolicoeur, J.-M. Brassard, and **F. Messier.** 1986. Predicting and correcting helicopter counts of moose with observations made from fixed-wing aircraft in southern Québec. Journal of Applied Ecology 23: 751-761.

Cumming, H. G., and **D. B. Beange.** 1993. Survival of woodland caribou in commercial forests of northern Ontario. Forestry Chronicle 69: 579-588.

Cumming, H. G., D. B. Beange, and **G. Lavoie.** 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. Rangifer, Special Issue 9: 81-94.

Edmonds, E. J. 1988. Population status, distribution and movements of woodland caribou in west central Alberta. Canadian Journal of Zoology 66: 817-826.

Farnell, R., N. Barichello, K. Egli, and **G. Kuzyk.** 1996. Population ecology of two woodland caribou herds in the southern Yukon. Rangifer, Special Issue 9: 63-72.

Folinsbee, J. D. 1979. Distribution et abondance passées et présentes du caribou (*Rangifer tarandus*) au Labrador méridional et dans les régions adjacentes du Québec. Recherches Amérindiennes au Québec 9: 37-46.

Gasaway, W. C., and **S. D. Dubois.** 1987. Estimating moose population parameters. Swedish Wildlife Research, Supplement 1: 603-617.

Heard, D., and **J.-P. Ouellet.** 1994. Dynamics of an introduced caribou population. Arctic 47: 88-95.

Mallory, F. F., and **T. L. Hillis.** 1998. Demographic characteristics of circumpolar caribou populations: ecotypes, ecological constraints/releases, and population dynamics. Rangifer, Special Issue 10: 49-60.

Moisan, G. 1957. Le caribou de Gaspé. III: Analyse de la population et plan d'aménagement. Naturaliste Canadien 84: 5-27.

Paré, M. 1987. Effets du remplissage d'un réservoir hydroélectrique sur la population de caribous de Caniapiscau. M.Sc. thesis, Université Laval. Québec, Québec. 141 pages.

Rettie, W. J., and **F. Messier.** 1998. Dynamics of Woodland caribou populations at the southern limit of their range in Saskatchewan. Canadian Journal of Zoology 76: 251-259.

Rivest, L.-P., S. Couturier, and **H. Crépeau.** 1994. Statistical methods for estimating caribou abundance using post-calving aggregations detected by radiotelemetry. Biometrics 54: 865-876.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology 70: 1494-1503.

Snedecor, G. W., and **W. G. Cochran.** 1971. Méthodes statistiques, 6e édition. Association de coordination technique agricole. Paris, France. 649 pages.

Stuart-Smith, A. K., C. J. A. Bradshaw, S. Boutin, D. M. Hebert, and **A. B. Rippin**. 1997. Woodland caribou relative to landscape pattern in northeastern Alberta. Journal of Wildlife Management 61: 622-633.

Received 30 October 2001
Accepted 12 February 2004

Subtidal Hydroids (Cnidaria) of Northumberland Strait, Atlantic Canada, with Observations on Their Life Cycles and Distributions

DALE R. CALDER

Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6 Canada; and Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1 Canada.

Calder, Dale R. 2003. Subtidal hydroids (Cnidaria) of Northumberland Strait, Atlantic Canada, with observations on their life cycles and distributions. Canadian Field-Naturalist 117(4): 555-564.

Hydroids were examined in collections from a biological survey of Northumberland Strait undertaken by Fisheries and Oceans Canada from June to August 1975. No investigations have been undertaken previously on hydroids of the study area. Forty-eight species referable to 12 families were present in the samples, with Sertulariidae dominating in both numbers of species (12) and frequency. Gonophores were found in 30 of the species. As usual in hydroids of higher latitudes, a majority of those represented do not have a medusa stage in their life cycle. Gonophores in 42 of the 48 species are known to be fixed sporosacs while free medusae or medusoids occur in only six. Two major species groups were distinguished in a numerical analysis of hydroid species/station data. One of these groups included the three most ubiquitous species (*Calycella syringa, Hydrallmania falcata, Sertularia latiuscula*) together with 15 others most prevalent in samples from shallower (<20 m) and warmer stations. The second group included species occurring primarily in samples from stations in deeper (>20 m) and mostly colder waters. Two species (*Lafoeina tenuis, Halecium lankesteri*) are new to the Atlantic coast of North America. Eight others (*Bougainvillia* sp., *Eudendrium dispar, Eudendrium ramosum, Cuspidella humilis, Opercularella pumila, Halecium scutum, Halecium sessile, Diphasia fallax*) are reported in the southwestern Gulf of St. Lawrence for the first time. The subtidal hydroid fauna in open waters of Northumberland Strait is a cold-water assemblage typical of the boreal zone in the western North Atlantic, and no relict warm-temperate species were found.

Key Words: hydroids, Cnidaria, Hydrozoa, Northumberland Strait, Prince Edward Island, Nova Scotia, New Brunswick, Gulf of St. Lawrence, reproduction, zoogeography.

Research on hydroids in Atlantic Canada began with Stimpson's (1854) synopsis of marine invertebrates in waters around Grand Manan Island, at the mouth of the Bay of Fundy, New Brunswick. Since then, however, fewer than two-dozen systematic accounts have been published on hydroids of the region. Most available knowledge was summarized in a guidebook, now more than six decades old, on species of the Atlantic coast of North America (Fraser 1944). Original information on hydroids of the southwestern Gulf of St. Lawrence is limited to five reports (Whiteaves 1901; Stafford 1912; Fraser 1926, 1927, 1944). None of these dealt with the fauna of Northumberland Strait, a sea channel separating Prince Edward Island from New Brunswick and Nova Scotia.

The southwestern Gulf of St. Lawrence, including Northumberland Strait, is biologically productive and of longstanding biogeographic interest (Ganong 1890). Being relatively shallow, waters undergo a wide annual range of temperature. Ice forms in the area during winter, while surface temperatures may approach or exceed 20°C in summer. As a result, a number of eurytopic temperate to warm-temperate species (e.g., the molluscs *Crassostrea virginica, Mercenaria mercenaria, Mulinia lateralis*, and *Urosalpinx cinerea*, the barnacle *Balanus improvisus*, the decapods *Ovalipes ocellatus* and *Rithropanopeus harrisii*, and the estuarine hydroid *Garveia franciscana*) occur in some localities. These invertebrates, considered relicts of a warmer period, are generally thought to be isolated from principal populations of their species occurring further south along the east coast of the United States by perpetually cold waters along much of the outer coast of Nova Scotia, the lower Bay of Fundy, and the northeastern Gulf of Maine (Ganong 1890; Whiteaves 1901; Fraser 1926; Bousfield 1960; Bousfield and Thomas 1975).

Objectives of this study were to census the subtidal hydroids of Northumberland Strait in the southwestern Gulf of St. Lawrence, and to determine their reproductive states, predominant life cycle patterns, and geographic affinities.

Materials and Methods

Materials examined were collected as part of the 1975 Northumberland Strait Project undertaken by the St. Andrews Biological Station, Fisheries and Oceans Canada. Marine invertebrates from this biological survey, including the hydroids studied here, were subsequently deposited at the Royal Ontario Museum (Carson 1985). Ninety-six stations were occupied between June and August 1975, during R/V *Harengus* Cruise Number 120, along a series of 13 transects extending across the strait in sequence from its northwestern to northeastern entrances into the Gulf of St. Lawrence. Samples of epibenthos were collected by beam trawl

TABLE 1. Stations in Northumberland Strait, eastern Canada, at which hydroids were collected during R/V *Harengus* cruise 120, 1975. BT = beam trawl; SD = scallop drag; NR = not recorded.

Station	Date	North Latitude	West Longitude	Gear	Depth (m)	Temp. (°C)	Bottom Type	Number of Species
Northwestern Sector								
2	11-VI-75	46°57'45"	64°45'15"	BT	13	11.0	NR	6
3	11-VI-75	46°57'45"	64°39'10"	BT	22	13.0	sandy	11
4	11-VI-75	46°57'45"	64°33'40"	BT	23	6.7	sandy	6
5	12-VI-75	46°57''45"	64°25'15"	BT	36	6.6	sandy/muddy	2
10	18-VI-75	46°52'40"	64°16'15"	BT	16	9.8	NR	4
11	18-VI-75	46°52'20"	64°22'15"	BT	29	2.5	NR	9
12	02-VII-75	46°52'15"	64°24'45"	BT	29	9.0	shell/gravel/boulders	13
13	02-VII-75	46°51'30"	64°39'50"	BT	25	10.5	NR	18
14	02-VII-75	46°51'20"	64°42'40"	BT	18	12.6	boulders	14
18	03-VII-75	46°43'40"	64°40'00"	SD	18	11.7	boulders	19
21	04-VII-75	46°44'00"	64°32'30"	SD	22	12.2	NR	8
22	04-VII-75	46°44'10"	64°30'10"	SD	25	12.0	mud/gravel/shell	14
24	04-VII-75	46°44'30"	64°23'30"	SD	11	15.5	boulders	12
West-central Sector								
25	04-VII-75	46°36'20"	64°23'25"	SD	07	17.0	shell/gravel/boulders	12
26	01-VII-75	46°35'35"	64°24'00"	BT	13	14.2	NR	4
30	26-VI-75	46°27'25"	64°30'05"	BT	09	14.1	sand	6
31	26-VI-75	46°26'30"	64°30'55"	BT	09	15.3	sand	12
32	26-VI-75	46°23'10"	64°33'20"	SD	05	16.2	sand	5
33	13-VI-75	46°17'15"	64°29'00"	BT	22	16.8	sand/mud	1
34	13-VI-75	46°18'35"	64°25'00"	BT	09	10.7	sand/mud	8
35	13-VI-75	46°19'20"	64°22'30"	BT	14	11.4	sand/mud	14
36	13-VI-75	46°20'15"	64°20'00"	BT	14	11.4	shell/gravel/sand	2
38	10-VI-75	46°22'05"	64°14'05"	BT	13	10.8	shell/gravel/sand	7
40	05-VI-75	46°24'00"	64°08'35"	BT	07	11.5	shell/gravel/sand	6
42	03-VI-75	46°18'00"	63°52'30"	BT	14	11.5	sand	11
43	03-VI-75	46°14'10"	63°54'15"	BT	22	11.4	mud	7
44	03-VI-75	46°11'45"	63°55'15"	BT	11	11.6	sand	8
45	24-VI-75	46°07'45"	63°45'10"	BT	09	15.1	sand/mud	6
46	24-VI-75	46°09'30"	63°45'30"	SD	29	13.5	shell/gravel/sand	11
48	24-VI-75	46°15'00"	63°43'00"	BT	09	14.6	shell/gravel/sand	14
East-central Sector								
49	10-VII-75	46°08'05"	63°19'15"	BT	09	14.8	sand/mud	4
52	09-VII-75	46°01'45"	63°27'50"	BT	22	11.0	mud	2
59	16-VII-75	45°54'10"	63°04'40"	BT	31	10.9	NR	1
60	18-VII-75	45°56'30"	63°05'15"	BT	27	10.8	mud	2
61	18-VII-75	45°58'30"	63°05'14"	BT	22	14.5	mud	12
62	18-VII-75	45°59'05"	63°05'50"	BT	22	13.5	mud	6
65	30-VII-75	45°56'50"	62°44'30"	BT	09	12.3	shell/gravel/sand	7
66	30-VII-75	45°55'45"	62°43'50"	BT	31	7.6	mud	14
67	30-VII-75	45°55'15"	62°40'40"	SD	29	10.9	mud	17
68	30-VII-75	45°49'30"	62°39'30"	SD	20	12.8	mud	8
71	24-VII-75	45°43'40"	62°35'40"	BT	09	16.2	sand	1
72	24-VII-75	45°43'00"	62°35'00"	SD	14	17.0	mud	2
73	10-VIII-75	45°46'15"	62°10'45"	BT	14	14.6	sand	11
74	10-VIII-75	45°47'00"	62°11'40"	BT	29	7.6	mud	3
75	10-VIII-75	45°48'10"	62°13'00"	BT	32	6.2	mud	2
76	31-VII-75	45°52'45"	62°18'40"	BT	31	5.3	mud	5
78	31-VII-75	45°56'15"	62°23'30"	BT	36	6.1	mud	17
79	31-VII-75	45°57'15"	62°24'00"	BT	36	3.4	mud	1
80	31-VII-75	45°59'40"	62°27'15"	BT	14	11.6	sand/mud	10
87	21-VII-75	45°51'15"	62°01'15"	BT	25	19.0	mud	1
Northeastern Sector								
84	24-VII-75	46°03'45"	62°16'45"	BT	34	13.5	mud	9
86	24-VII-75	46°01'00"	62°12'20"	BT	34	14.0	mud	10
90	22-VII-75	45°54'30"	61°53'10"	SD	32	15.0	mud	1
91	22-VII-75	46°00'10"	61°57'30"	BT	49	10.0	mud	1
92	22-VII-75	46°04'45"	62°00'00"	SD	32	12.0	boulders	10

at 68 of the stations, and by scallop drag at the remaining 28. Hydroids were identified in samples from 55 of the stations (Table 1), and presence or absence of gonophores was determined.

Species associations in the collection were determined by numerical analysis (Rohlf 1990) of a data matrix recording presence or absence of each of 48 species encountered overall at each of 55 stations. Qualitative similarity coefficients were computed using the SIMQUAL program, employing the PHI coefficient. Inverse (species-group) cluster analysis was then undertaken by the SAHN program employing the UPGMA clustering method and using a beta value of –0.25.

Study Area

Northumberland Strait separates Prince Edward Island from New Brunswick and Nova Scotia in Atlantic Canada. Some 330 km in length, it comprises a moderately sheltered central region with funnel-shaped openings to the Gulf of St. Lawrence at its northwestern and northeastern ends. Minimum width across the strait is 12 km, maximum depth is approximately 50 m, tidal range averages about 3 m, salinities are typically euhaline (>30‰), and the shoreline is predominantly sandy. Surface waters of the strait freeze over in winter but approach or exceed 20°C in summer.

At 96 stations occupied in late spring and summer during the 1975 Northumberland Strait Project, water temperatures varied from 2.5°C (Station 11) to 19.5°C (Stations 81, 89). Station depths ranged from 5 m (Stations 32, 57) to 49 m (Station 91). Bottoms consisted primarily of boulders or sand in the Northwestern Sector of the strait (Stations 1-24, north of 46°40'N), shell/gravel/sand or sand in the West-central Sector (Stations 25-48, eastward to 63°40'W), mud in the East-central Sector (Stations 49-80, 87, and 88, eastward to a line from Cape Bear [46°00'N, 62°28'W] to Cape George [61°56'N, 45°53'W]), and mud or boulders in the Northeastern Sector (Stations 81-86 and 89-96, northeast of the East-central Sector).

Results

Hydroid diversity in Northumberland Strait was moderately low, with 48 species identified in the samples (Table 2). Leptothecates accounted for 40 of these and anthoathecates eight. Five of the species (*Calycella syringa, Hydrallmania falcata, Sertularia latiuscula, Sertularella polyzonias, Obelia longissima*), all leptothecates, were found at 24 or more of the 96 stations. These and six other ubiquitous species (*Symplectoscyphus tricuspidatus, Abietinaria abietina, Hydractinia polyclina, Rhizocaulus verticillatus, Gonothyraea loveni, Lafoea dumosa*) occurred in samples from all four sectors of the strait (Northwestern, West-central, East-central, and Northeastern). Two species (*Lafoeina tenuis, Halecium lankesteri*) are new to the Atlantic coast of North America. Eight others (*Bougainvillia* sp., *Eudendrium dispar, Eudendrium ramosum, Cuspidella humilis, Opercularella pumila, Halecium scutum, Halecium sessile, Diphasia fallax*) are reported in waters of the southwestern Gulf of St. Lawrence for the first time. Of the 12 families of hydroids represented in the collection, Sertulariidae dominated both in numbers of species (12) and frequency in the samples (Table 2).

Colonies with gonophores were observed in 30 of the 48 species from the collections (Table 2), although most specimens were infertile. Of 427 records of hydroid species, gonophores were present in 108 (25%) but absent or undetected in the remaining 319 (75%). Fertile colonies were noted in 26 of 50 specimen records of anthoathecate species but in only 82 of 377 records of leptothecate species.

The fauna was divisible ecologically into two major species groups (Table 2) based on results of an inverse cluster analysis. Group I included the three most ubiquitous species (*Calycella syringa, Hydrallmania falcata, Sertularia latiuscula*) as well as 15 others associated for the most part with stations in shallower and somewhat warmer waters (mean depth 15.4 m; mean water temperature 12.5°C). Group II species, 30 in number, were generally associated with deeper and colder sites (mean depth 23.1 m; mean water temperature 11.3°C). Eight of these 30 (*Keratosum maximum, Lafoeina tenuis, Halecium muricatum, Halecium scutum, Campanularia groenlandica, Orthopyxis integra, Grammaria gracilis, Lafoea gracillima*) were found only at stations in the more exposed northwestern and northeastern entrances of the strait.

Discussion

Of the 48 species identified here from Northumberland Strait, 10 have not been reported before from the southwestern Gulf of St. Lawrence region (*Bougainvillia* sp., *Eudendrium dispar, Eudendrium ramosum, Cuspidella humilis, Lafoeina tenuis, Opercularella pumila, Halecium lankesteri, Halecium scutum, Halecium sessile, Diphasia fallax*). All of them, however, are regarded as typical of boreal Atlantic waters (Table 2) and they are unlikely to have been recently introduced. Hydroid species reported from other localities in the southwestern gulf, but not found here, are listed in Table 3.

Gonophores were observed in 30 of the species. It is not known whether colonies of the remaining 18 are fertile during summer in the area. Numerous factors, including water temperature, nutrition, environmental stresses, and in some species even lunar and diurnal cycles (e.g., Elmhirst 1925; Ballard 1942; Stebbing 1980; Arai 1987; Calder 1990, 1991; Cornelius 1990; Piraino 1991; Gili and Hughes 1995), are likely to influence physiological functions such as the periodicity and frequency of gonophore production and gamete or medusa release. Gonophore formation in hydroids appears to be decidedly seasonal in spe-

TABLE 2. Hydroid species in samples from Northumberland Strait, with station records and gonophore types. Numbers in bold indicate stations with samples having hydroids with gonophores. Gonophore types: Fx=fixed; Me=medusa; Md=medusoid. Species Group I=shallow-water assemblage; Species Group II= deeper-water assemblage.

Species	Stations	Type of Gonophore Fx	Me	Md	Species Group	Known Range, Western North Atlantic Neritic Zone
ORDER ANTHOATHECATA						
Family Bougainvilliidae						
Bougainvillia sp.	**46**, 80		+		I	
Dicoryne conferta (Alder, 1856)	5, **13**, **14**, **35**, **84**	+			II	Gulf of St. Lawrence—Massachusetts Bay
Family Hydractiniidae						
Hydractinia polyclina (L. Agassiz, 1860)	4, 5, **11**, **12**, **13**, **14**, **31**, **32**, **33**, 35, **36**, **38**, **71**, 80, 87, **90**, 91	+			II	Gulf of St. Lawrence—New England
Family Eudendriidae						
Eudendrium album Nutting, 1896	61, 68, **73**, 84	+			I	Gulf of St. Lawrence—Florida
Eudendrium dispar L. Agassiz, 1862	**18**, 38	+			II	Gulf of St. Lawrence—Block Island Sound
Eudendrium ramosum (Linnaeus, 1758)	**3**, 12, 13, 24, 25, 26, 30, **31**, 34, 35, **42**, 43, **45**, **46**, 48, **67**, 78	+			I	Gulf of St. Lawrence—Chesapeake Bay
Family Corymorphidae						
Corymorpha pendula L. Agassiz, 1862	**78**	+			II	Gulf of St. Lawrence—Block Island Sound
Family Tubulariidae						
Ectopleura larynx (Ellis & Solander, 1786)	18, **73**	+			II	Gulf of St. Lawrence—Long Island Sound
ORDER LEPTOTHECATA						
Family Calycellidae						
Calycella syringa (Linnaeus, 1767)	2, 3, 10, 11, 12, 13, **14**, **18**, 22, 24, 25, 26, 30, 31, 32, 34, **35**, 36, 38, 40, **42**, **43**, 44, 45, **46**, **48**, 49, 61, 62, 66, 67, 68, 73, 76, 80, 84, 86, **92**	+			I	Arctic Ocean—Long Island Sound
Family Incertae Sedis						
Cuspidella humilis Hincks, 1866	44		+		I	Arctic Ocean—George's Bank
Keratosum maximum (Levinsen, 1893)	12	+			II	Arctic Ocean—Cape Cod
Lafoeina tenuis G. O. Sars, 1874	11	+			II	Northumberland Strait (this study)
Family Phialellidae						
Opercularella lacerata (Johnston, 1847)	31, 32, 42, 48	+			I	Arctic Ocean—Long Island Sound
Opercularella pumila Clark, 1875	**26**, 31, **35**, 40, **44**	+			I	Northumberland Strait—Chesapeake Bay
Family Haleciidae						
Halecium beanii (Johnston, 1838)	35	+			II	Gulf of St. Lawrence—Long Island Sound
Halecium halecinum (Linnaeus, 1758)	38, 44, **46**, **61**, **68**	+			I	Strait of Belle Isle—Chesapeake Bay
Halecium labrosum Alder, 1859	42, 48, 78	+			I	Frobisher Bay—George's Bank
Halecium lankesteri (Bourne, 1890)	42	+			I	Northumberland Strait (this study)

TABLE 2. *(continued)* Hydroid species in samples from Northumberland Strait, with station records and gonophore types. Numbers in bold indicate stations with samples having hydroids with gonophores. Gonophore types: Fx=fixed; Me=medusa; Md=medusoid. Species Group I=shallow-water assemblage; Species Group II= deeper-water assemblage.

Species	Stations	Type of Gonophore			Species Group	Known Range, Western North Atlantic Neritic Zone
		Fx	Me	Md		
Halecium muricatum (Ellis & Solander, 1786)	**2**, **3**, **13**, 14, 18, 92	+			II	Arctic Ocean—Cape Cod
Halecium scutum Clark, 1877	**3**	+			II	Frobisher Bay—Northumberland Strait
Halecium sessile Norman, 1867	65, 66, 67	+			II	Gulf of St. Lawrence—Gulf of Maine
Halecium undulatum Billard, 1922	46, 66, 80	+			I	Frobisher Bay—Northumberland Strait
Family Campanulariidae						
Campanularia groenlandica Levinsen, 1893	22, 92	+			II	Arctic Ocean—Cape Cod
Campanularia volubilis (Linnaeus, 1758)	13, 18, 21, 22, 48, 66, 67	+			II	Arctic Ocean—Block Island Sound
Orthopyxis integra (Macgillivray, 1842)	92			+	II	Arctic Ocean—Vineyard Sound
Clytia hemisphaerica (Linnaeus, 1767)	24, 25, 30, 31, 34, 35, 38, 42, 46, 48, 49, **61**, **73**		+		I	Labrador—Florida
Gonothyraea loveni (Allman, 1859)	14, 22, 35, 40, 42, 43, 46, 48, 49, 61, 66, 86	+			I	Foxe Basin—South Carolina
Laomedea neglecta Alder, 1856	**48**, 73	+			I	Gulf of St. Lawrence—Woods Hole
Obelia geniculata (Linnaeus, 1758)	**31**, 32, 34, 35, 40, 44, 45, **48**, 52,75		+		I	northern Hudson Bay—Caribbean Sea
Obelia longissima auct.	12, 13, 18, 24, 25, 31, 34, 35, 40, 42, 46, 48, **61**, 62, 66, 67, 68, 72, 73, 74, 78, 80, 84, 86		+		II	Ungava Bay—South Carolina
Rhizocaulus verticillatus (Linnaeus, 1758)	4, **12**, 14, **18**, 22, 46, 60, **61**, 62, **67**, 76, 78, 84, **86**	+			II	Frobisher Bay—Long Island Sound
Family Lafoeidae						
Filellum serpens (Hassall, 1848)	2, 11, 13, 14, 18, 22, 24, 61, 62, 65, 66, **67**, 78, **92**	+			II	northern Foxe Basin—Buzzard's Bay
Grammaria gracilis Stimpson, 1854	3, 4, 13, 86	+			II	Foxe Basin—Bay of Fundy
Lafoea dumosa (Fleming, 1828)	11, 12, 13, 18, 22, 25, 67, 78, 86	+			II	Ungava Bay—Mid-Atlantic Bight
Lafoea gracillima (Alder, 1856)	**18**, 84	+			II	Arctic Ocean—Nantucket Sound
Family Sertulariidae						
Abietinaria abietina (Linnaeus, 1758)	**2**, 3, **12**, 13, 14, **18**, 21, 22, 24, 25, 65, 66, 67, 68, 76, 78, 80, **92**	+			II	northern Hudson Bay—Nantucket Sound
Abietinaria pulchra (Nutting, 1904)	**18**, **25**, **35**, 43, **73**, 78	+			II	Hudson Bay—Gulf of St. Lawrence
Diphasia fallax (Johnston, 1847)	12, 13, 14, 18, 21, 22, 24, **25**, **65**, 66, 80	+			II	Northumberland Strait—Block Island Sound
Hydrallmania falcata (Linnaeus, 1758)	**2**, 3, **4**, 10, **11**, **12**, 13, 14, 18, **21**, 22, **24**, 25, **30**, **31**, **34**, **35**,	+			I	Strait of Belle Isle—Long Island Sound

TABLE 2. *(continued)* Hydroid species in samples from Northumberland Strait, with station records and gonophore types. Numbers in bold indicate stations with samples having hydroids with gonophores. Gonophore types: Fx=fixed; Me=medusa; Md=medusoid. Species Group I=shallow-water assemblage; Species Group II= deeper-water assemblage.

Species	Stations	Type of Gonophore			Species Group	Known Range, Western North Atlantic Neritic Zone
		Fx	Me	Md		
	38, **42**, **43**, **44**, 45, 46, 48, 52, **61**, 62, 65, 66, 67, 68, 72, 73, **78**, **80**, 86					
Pericladium mirabile (Verrill, 1873)	4, **11**, 13, 18, 22, 67	+			II	Hudson Strait—George's Bank
Sertularella polyzonias (Linnaeus, 1758)	3, 10, 11, 13, 14, 18, 21, 22, **24**, **25**, 59, 60, 61, **65**, **66**, **67**, 68, 76, 78, 79, 80, 84, 86, 92	+			II	Foxe Basin—Long Island Sound
Sertularella rugosa (Linnaeus, 1758)	**2**, 24, 30, 31, 32, **34**, 35, 38, 42, 43, **44**, 45, **48**, 49, 73	+			I	Labrador—Long Island Sound
Sertularia cupressina Linnaeus,1758	12, 18, 24, 25, **43**, 66, 67, 68, 74, **78**	+			II	Labrador—Mid-Atlantic Bight
Sertularia fabricii Levinsen, 1893	48, **67**, **73**, **78**, **84**	+			II	Strait of Belle Isle—Block Island Sound
Sertularia latiuscula Stimpson, 1854	**3**, 4, 13, 14, **21**, 22, **24**, 26, 30, **31**, 34, **35**, 40, **42**, 44, 45, 46, 48, 61, 66, 67, 73, 75, 76, 78, 80, **84**, **86**, 92	+			I	Gulf of St. Lawrence—Mid-Atlantic Bight
Sertularia similis Clark, 1877	3, 12, 13, 14, 21, 67, 74, 78, 92	+			II	Foxe Basin—Mid-Atlantic Bight
Symplectoscyphus tricuspidatus (Alder, 1856)	3, 10, 11, 12, 13, 14, 18, 21, 22, 25, 31, 61, 62, 65, 66, 67, 78, 86, 92	+			II	Arctic Ocean—Long Island Sound
Thuiaria laxa Allman, 1874	18, 78	+			II	Strait of Belle Isle—Cape Cod
Gonophore Type, Totals		42	5	1		

TABLE 3. Additional species of hydroids reported from the southwestern Gulf of St. Lawrence region, eastern Canada, but not found in samples from R/V *Harengus* Cruise No. 120 to Northumberland Strait.

Species	Reported as:	Location	References
ORDER ANTHOATHECATA			
Family Cordylophoridae			
Cordylophora caspia (Pallas, 1771)	*Cordylophora lacustris*	Miramichi estuary, low salinity	Fraser 1926
Family Hydractiniidae			
Clava multicornis (Forsskål, 1775)	*Clava leptostyla*	Miramichi estuary	Fraser 1926
Hydractinia carica Bergh, 1887	*Hydractinia minuta*	Magdalen Islands	Fraser 1927
Family Bougainvilliidae			
Garveia brevis (Fraser, 1918)[1]	*Bimeria brevis*	Cape Breton: Pleasant Bay	Fraser 1927
Garveia franciscana (Torrey, 1902)	*Calyptospadix cerulea*	Miramichi estuary, low salinity	Fraser 1926
Family Pandeidae			
Leuckartiara octona (Fleming, 1823)	*Perigonimus sessilis*	Miramichi Bay area	Fraser 1926
Family Tubulariidae			
Ectopleura crocea (L. Agassiz, 1862)	*Tubularia crocea*	Miramichi Bay	Fraser 1926
Tubularia indivisa Linnaeus, 1758	*Tubularia indivisa*	Miramichi Bay	Fraser 1926
		Between Cape Breton and Magdalen Islands	Fraser 1927
Family Corynidae			
Sarsia tubulosa (M. Sars, 1835)	*Syncoryne mirabilis*	Miramichi estuary, shallow water	Fraser 1926
		Cape Breton: Pleasant Bay	Fraser 1927
ORDER LEPTOTHECATA			
Family Haleciidae			
Halecium curvicaule Lorenz, 1886	*Halecium curvicaule*	Cape Breton: N of Cheticamp Island	Fraser 1927
Family Campanulariidae			
Campanularia hincksii Alder, 1856	*Campanularia hincksi*	Miramichi estuary	Fraser 1926
Hartlaubella gelatinosa (Pallas, 1766)	*Campanularia gelatinosa*	Miramichi estuary	Fraser 1926
		Magdalen Islands	Fraser 1927
Family Lafoeidae			
Grammaria abietina (M. Sars, 1850)	*Grammaria abietina*	Miramichi estuary	Fraser 1926
		Cape Breton: N of Cheticamp Island	Fraser 1927
Lafoea fruticosa (M. Sars, 1850)	*Lafoea fruticosa*	Miramichi estuary	Fraser 1926
		Cape Breton: off Cheticamp Island	Fraser 1927
Family Sertulariidae			
Abietinaria kincaidi (Nutting, 1901)	*Diphasia kincaidi*	Miramichi estuary	Fraser 1926
Abietinaria thuiarioides (Clark, 1877)	*Thuiaria thuiarioides*	Miramichi estuary	Fraser 1926
		Magdalen Islands	Fraser 1927
Dynamena pumila (Linnaeus, 1758)	*Sertularia pumila*	Cape Breton: Eastern Harbour; Cheticamp Island	Fraser 1927
		Souris, Prince Edward Island	Fraser 1944
Sertularella tenella (Alder, 1857)	*Sertularella tenella*	Cape Breton: N of Cheticamp Island	Fraser 1927
Sertularia argentea Linnaeus, 1758	*Thuiaria argentea*	Northumberland Strait	Whiteaves 1901
	Thuiaria argentea	Miramichi estuary	Fraser 1926

TABLE 3. *(concluded)* Additional species of hydroids reported from the southwestern Gulf of St. Lawrence region, eastern Canada, but not found in samples from R/V *Harengus* Cruise No. 120 to Northumberland Strait.

Species	Reported as:	Location	References
Sertularia argentea Linnaeus, 1758	*Thuiaria argentea*	Northumberland Strait	Whiteaves 1901
	Thuiaria argentea	Miramichi estuary	Fraser 1926
	Thuiaria argentea	Cape Breton: off Cheticamp Island between Cape Breton and Magdalen Island; Magdalen Island	Fraser 1927
Thuiaria alternitheca (Levinsen, 1893)	*Selaginopsis alternitheca*	Cape Breton: N of Cheticamp Island	Fraser 1927
Thuiaria articulata (Pallas, 1766)	*Thuiaria kolaensis*	Miramichi estuary	Fraser 1926
		Cape Breton: N of Cheticamp Island	Fraser 1927
Thuiaria carica Levinsen, 1893	*Thuiaria carica*	Miramichi estuary	Fraser 1926
ORDER LIMNOMEDUSAE			
Family Olindiidae			
Monobrachium parasitum Mereschkowsky 1877	*Monobrachium parasiticum*	Cape Breton: off Cheticamp Island	Fraser 1927

[1] Doubtful species

cies from areas subjected to significant annual water temperature ranges. Moreover, the duration of gonophore production in such areas is often considerably shorter than the period of trophosome activity for a given species, indicating that the range of factors conducive to production of gonophores is narrower than for vegetative activity and asexual colony growth. For example, gonophores were observed an average of 16 weeks a year in warm-water hydroid species vegetatively active for an average of 30 weeks, and 23 weeks a year in cold-water species active over an average of 32 weeks in southern Chesapeake Bay, Virginia (Calder 1990). None of these species produced gonophores or were vegetatively active throughout the year. In some of the rarer species from Northumberland Strait, specimens with gonophores may have simply been missed. However, the restricted sampling period (June through early August) in an area where temperatures vary widely from one season to another may also have been a factor. Stenothermal cold-water hydroids, especially those ranging into much higher latitudes, may not produce gonophores in Northumberland Strait during the warmest time of year when sampling was undertaken.

Life cycles in only six of the species are known to include a free medusa (*Bougainvillia* sp., *Cuspidella humilis*, *Clytia hemisphaerica*, *Obelia geniculata*, *O. longissima*) or a medusoid (*Orthopyxis integra*). In the remaining 42, gonophores are fixed sporosacs (Table 2). Life cycles are abbreviated and gonophores fixed in seven of eight anthoathecate species and 35 of 40 leptothecates.

Correlations have long been noted between life cycle patterns of hydroids and their biotope. For example, fixed gonophores predominate among species living as obligate associates of the seagrass *Posidonia oceanica* in the Mediterranean (Philbert 1935; Picard 1952; Boero 1987) and asexual reproduction by stolonization is prevalent. Reduced dispersal in seagrass-inhabiting hydroids seems biologically advantageous because propagules tend to stay in the specialized habitat occupied by parent populations. Cornelius (1992a, b) and Calder (2000) noted that hydrozoans of oceanic islands and seamounts tended to be comprised largely of species with fixed gonophores instead of free medusae, thereby increasing the probability of larval retention within insular environments (see Johannesson 1988). Fixed gonophores were observed to be prevalent among hydroids living in cold waters along the western North Atlantic coast (Calder 1992), including the Gulf of St. Lawrence. By comparison, the proportion of species with a medusa stage in their life cycles was found to be greater at locations in lower latitudes, although hydroid species having free medusae outnumbered those having fixed gonophores only in temperate estuaries among localities studied. As with hydroids in high latitudes, including those of Northumberland Strait studied here, most species known from the deep-sea possess fixed gono-

phores (Vervoort 1966; Calder 1997; Calder and Vervoort 1998). Indeed, non-pelagic larval development generally predominates among benthic invertebrate species of both high latitudes and the abyss (e.g., see Thorson 1950; Gage and Tyler 1991). The suppression of pelagic larval development typical in the benthic fauna of these environments appears correlated at least in part with limited food availability for meroplanktonic stages, given the short growing season for phytoplankton in polar waters and the oligotrophic conditions prevailing in much of the deep sea. Such "attribute syndromes" were also noted and discussed in relation to epilithic and epizoic hydroid assemblages from heavily dredged scallop grounds in the Bay of Fundy (Henry and Kenchington 2004). Each kind of hydroid life cycle, whether fixed gonophores, reduced and ephemeral medusoids, or free medusae, seems to offer advantages and disadvantages depending upon the biological circumstances of individual species. It is thus apparent why reproduction by both fixed gonophores and free medusae has been retained in Hydrozoa, and why medusa suppression has evidently occurred independently a number of times in both anthoathecates and leptothecates.

Although waters of Northumberland Strait are relatively shallow, two species groups correlated at least in part with depth and water temperature were distinguished in a numerical analysis. Group I comprised an assemblage of 18 species, including a suite of 15 that were most prevalent in samples from shallower (<20 m) and somewhat warmer stations. The remaining three species of the group (*Calycella syringa, Hydrallmania falcata, Sertularia latiuscula*), all quite eurythermal, were the most ubiquitous hydroids in the collection. Group II species predominated at stations in deeper (>20 m) and typically colder waters, and several of them were either limited to or most frequent in samples from exposed stations in the two entrances of the strait. Earlier, two depth-related assemblages of hydroids had been recognized by Fraser (1926) in nearby waters of the Miramichi estuary, Miramichi Bay, and the adjacent Gulf of St. Lawrence. Fraser reported that the fauna from depths of less than 15 m in the Miramichi area included a number of species commonly ranging farther south, while more northern or arctic species were represented at depths of 15 m or greater.

Water temperatures in shallow areas of Northumberland Strait were mostly moderate during the study. Nevertheless, none of the hydroids examined here is considered a warm-water species with a disjunct distribution along this coast. The reported ranges of two hydroids (*Opercularella pumila, Diphasia fallax*) were extended northward on this coast to Northumberland Strait, but both are cold-temperate species whose distributions are unlikely to be discontinuous. With no fewer than 30 of the 48 species from this study extending into subarctic or even Arctic waters (Table 2), the subtidal hydroid fauna of the open strait is regarded here as an essentially cold-water (boreal) one. A marked zoogeographic affinity between hydroid assemblages of the southwestern Gulf of St. Lawrence (Miramichi and Cheticamp areas) with those of two continually cold-water areas elsewhere in Atlantic Canada (Canso, Nova Scotia; Passamaquoddy Bay, New Brunswick) was noted earlier (Calder 1992). A typically boreal fauna was also reported in a study of Bryozoa from the 1975 Northumberland Strait Project (Carson 1985).

Acknowledgments

All samples studied here were collected by staff of Fisheries and Oceans Canada, St. Andrews Biological Station, St. Andrews, New Brunswick. Michael Dadswell and Renate Carson arranged a transfer of the collection, together with collection data, to the Royal Ontario Museum, and I thank them both. The financial support of a research grant from the Natural Sciences and Engineering Research Council of Canada is acknowledged.

Literature Cited

Arai, M. N. 1987. Population ecology of the hydromedusae of Masset Inlet, British Columbia. Pages 107-116 *in* Modern trends in the systematics, ecology, and evolution of hydroids and hydromedusae. *Edited by* J. Bouillon, F. Boero, F. Cicogna, and P. F. S. Cornelius. Clarendon Press, Oxford.

Ballard, W. W. 1942. The mechanism for synchronous spawning in *Hydractinia* and *Pennaria*. Biological Bulletin (Woods Hole, Massachusetts) 82: 329-339.

Boero, F. 1987. Evolutionary implications of habitat selection in the hydroids of *Posidonia oceanica* meadows. Pages 251-256 *in* Modern trends in the systematics, ecology, and evolution of hydroids and hydromedusae. *Edited by* J. Bouillon, F. Boero, F. Cicogna, and P. F. S. Cornelius. Clarendon Press, Oxford.

Bousfield, E. L. 1960. Canadian Atlantic sea shells. National Museum of Canada, Ottawa.

Bousfield, E. L., and **M. L. H. Thomas.** 1975. Postglacial changes in distribution of littoral marine invertebrates in the Canadian Atlantic region. Proceedings of the Nova Scotia Institute of Science 27, supplement 3: 47-60.

Calder, D. R. 1990. Seasonal cycles of activity and inactivity in some hydroids from Virginia and South Carolina, USA. Canadian Journal of Zoology 68: 442-450.

Calder, D. R. 1991. Vertical zonation of the hydroid *Dynamena crisioides* (Hydrozoa, Sertulariidae) in a mangrove ecosystem at Twin Cays, Belize. Canadian Journal of Zoology 69: 2293-2999.

Calder, D. R. 1992. Similarity analysis of hydroid assemblages along a latitudinal gradient in the western North Atlantic. Canadian Journal of Zoology 70: 1078-1085.

Calder, D. R. 1997. Synopsis of hydroids from 1000 m and deeper in the western North Atlantic. Proceedings of the 6th International Conference on Coelenterate Biology 1995: 85-90.

Calder, D. R. 2000. Assemblages of hydroids (Cnidaria) from three seamounts near Bermuda in the western North Atlantic. Deep-Sea Research I 47: 1125-1139.

Calder, D. R., and **W. Vervoort.** 1998. Some hydroids (Cnidaria: Hydrozoa) from the Mid-Atlantic Ridge, in the North Atlantic Ocean. Zoologische Verhandelingen (Leiden) 319: 1-66.

Carson, R. 1985. Bryozoans of Northumberland Strait, Gulf of St. Lawrence. Pages 59-64 *in* Bryozoa: Ordovician to Recent. *Edited by* C. Nielsen and G. P. Larwood. Olsen and Olsen, Fredensborg.

Cornelius, P. F. S. 1990. Evolution in leptolid life-cycles (Cnidaria: Hydroida). Journal of Natural History 24: 579-594.

Cornelius, P. F. S. 1992a. Medusa loss in leptolid Hydrozoa (Cnidaria), hydroid rafting, and abbreviated life-cycles among their remote-island faunae: an interim review. Scientia Marina 56(2/3): 245-261.

Cornelius, P. F. S. 1992b. The Azores hydroid fauna and its origin, with discussion of rafting and medusa suppression. Arquipélago, Life and Earth Sciences 10: 75-99.

Elmhirst, R. 1925. Lunar periodicity in *Obelia*. Nature (London) 116: 358-359.

Fraser, C. M. 1926. Hydroids of the Miramichi Estuary collected in 1918. Transactions of the Royal Society of Canada, 3rd series, 20 (section 5): 209-214.

Fraser, C. M. 1927. The hydroids of the Cheticamp Expedition of 1917. Contributions to Canadian Biology and Fisheries 3: 325-329.

Fraser, C. M. 1944. Hydroids of the Atlantic coast of North America. University of Toronto Press, Toronto.

Gage, J. D., and **P. A. Tyler.** 1991. Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge.

Ganong, W. F. 1890. Southern invertebrates on the shores of Acadia. Transactions of the Royal Society of Canada 8(4): 167-185.

Gili, J.-M., and **R. G. Hughes.** 1995. The ecology of marine benthic hydroids. Annual Review of Oceanography and Marine Biology 33: 351-426.

Henry, L.-A., and **E. Kenchington.** 2004. Differences between epilithic and epizoic hydroid assemblages from commercial scallop grounds in the Bay of Fundy, northwest Atlantic. Marine Ecology Progress Series 266: 123-134.

Johannesson, K. 1988. The Paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*)? Marine Biology 99: 507-513.

Philbert, M. 1935. Le phénomène de stolonisation chez trois espèces d'hydraires fixes sur des posidonies en Méditerranée. Bulletin de l'Institut d'Océanographie de Monaco 663: 1-8.

Picard, J. 1952. Les hydrozoaires des herbiers de zostéracées des côtes françaises de la Méditerranée. Vie et Milieu 2 (supplément): 217-233.

Piraino, S. 1991. The adaptive pattern of growth and reproduction of the colonial hydroid *Clavopsella michaeli*. Hydrobiologia 216/217: 229-234.

Rohlf, F. J. 1990. NTSYS-pc. Numerical taxonomy and multivariate analysis system, version 1.60. Applied Biostatistics Inc., Setauket, New York.

Stafford, J. 1912. On the fauna of the Atlantic coast of Canada. Fourth report. Contributions to Canadian Biology 1906-1910: 69-78.

Stebbing, A. R. D. 1980. Increase in gonozooid frequency as an adaptive response to stress in *Campanularia flexuosa*. Pages 27-32 *in* Developmental and cellular biology of coelenterates. *Edited by* P. Tardent and R. Tardent. Elsevier North-Holland Biomedical Press, Amsterdam.

Stimpson, W. 1854. Synopsis of the marine Invertebrata of Grand Manan; or the region about the mouth of the Bay of Fundy, New Brunswick. Smithsonian Contributions to Knowledge 6(5): 1-67.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25: 1-45.

Vervoort, W. 1966. Bathyal and abyssal hydroids. Galathea Report 8: 97-174.

Whiteaves, J. F. 1901. Catalogue of the marine Invertebrata of eastern Canada. Geological Survey of Canada Separate Report Number 722: 1-272.

Received 17 December 2001
Accepted 5 April 2004

Seasonal Habitat Use and Movements of Mountain Goats, *Oreamnos americanus,* in East-central British Columbia

KIM G. POOLE[1] and DOUGLAS C. HEARD[2]

[1] Aurora Wildlife Research, 2305 Annable Rd., Nelson, British Columbia V1L 6K4 Canada; e-mail: klpoole@shaw.ca
[2] British Columbia Ministry of Water, Land and Air Protection, 4051 18th Avenue, Prince George, British Columbia V2N 1B3 Canada; e-mail: doug.heard@gems7.gov.bc.ca

Poole, Kim G., and Douglas C. Heard. 2003. Seasonal habitat use and movements of Mountain Goats, *Oreamnos americanus,* in east-central British Columbia. Canadian Field-Naturalist 117(4): 565-576.

To identify the potential for adverse effects of forest development on Mountain Goats (*Oreamnos americanus*), we documented the patterns of forest use by goats and the factors influencing goat habitat use. We used a combination of 15 very high frequency (VHF) and six global positioning system (GPS) radiocollars to document the distribution and movements of 21 (15 female, 6 male) goats from 1997 to 1999 in the mountains surrounding the Robson Valley in east-central British Columbia. Because canopy closure reduces the likelihood that a GPS receiver will obtain a location fix, we estimated that GPS collars underrepresented forest use by about 23%. Three goats used separate winter and summer ranges separated by 8–13 km, while most simply exhibited seasonal shifts in elevation. In winter, goats were more often at lower elevations, in commercial forest stands, on southerly aspects, and moved less each hour and over the course of the winter. Goat use declined in areas >500 m from escape terrain and goats were found lower in elevation from evening to dawn compared to daylight hours. Collared goats used high elevation licks, which were either within their home range, or in two cases, 6 and 14 km from their typical home range. We documented use of known mid-elevation mineral licks by three collared goats, but no use of known low elevation (valley bottom and lower slopes) mineral licks. Robson Valley goats appeared to be at relatively low risk from disturbances related to logging, because although forest use was documented during winter, it occurred primarily on high elevation, steep slopes where trees are currently of low commercial value, and goats made little use of low elevation mineral licks. We recommend that in this area a forested buffer of 500 m around cliffs be left to reduce the possibility of adverse effects on goats especially, on southerly aspects above 1300 m.

Key Words: Mountain Goats, *Oreamnos americanus,* British Columbia, distribution, habitat use, home range, mineral licks, movements.

Although often residents of steep alpine terrain, Mountain Goats (*Oreamnos americanus*; hereafter, goats) use montane forests for food and cover during fall (Demarchi et al. 2000) and winter (Hebert and Turnbull 1977; McCrory et al. 1977; Adams and Bailey 1983; Fox and Smith 1988; Gilbert and Raedeke 1992), when moving to low elevation mineral licks in spring and summer (Hebert and Cowan 1971; Singer and Doherty 1985; Hopkins et al. 1992), and occasionally when moving among high elevation ranges. Environmental changes resulting from forestry operations may, therefore, affect goats, but are still poorly understood (Côté and Festa-Bianchet 2003). Forestry development can increase access and the loss and fragmentation of habitat. Because goats rarely venture far from cliffs that are steep enough to provide a refuge from terrestrial predators (Smith 1986; Haynes 1992), forestry development plans must also consider those terrain features.

In the mountains surrounding the Robson Valley in east-central British Columbia, Canada, forestry activities are encroaching on goat range, pushing farther into previously-undisturbed side valleys of the Fraser River and Kinbasket Reservoir and higher up hillsides toward the alpine zone (Slocan Forest Products Ltd., Valemount Division, Five-year Harvest Plan, April 1997; C. Ritchie, British Columbia Ministry of Environment, Lands and Parks [MELP], Prince George, personal communication). To identify the potential for adverse effects of logging on goat populations, we examined the patterns of movements and forest use by goats with the expectation that forest use by goats would primarily be during the period when they used low elevation mineral licks. Little is known about seasonal movements of goats (Côté and Festa-Bianchet 2003), information which could affect their association with forestry operations. We used a combination of very high frequency (VHF) and global positioning system (GPS) radiocollars to document the distribution and movements of goats. The long battery life and relatively low cost of conventional VHF radiocollars allowed us to monitor 15 goats one to four times each month over two years (1997–1999), providing general movement information throughout the year. The high relocation frequency of GPS collars, during both day and night (Poole and Heard 1998), allowed us to determine the detailed movements of six goats but for a shorter duration.

Study Area

Our study area encompassed the mountains surrounding approximately 190 linear km of the Robson Valley in east-central British Columbia (centred on 52° 49' N, 119° 15'W; Figure 1). The Rocky Mountains run along the northeast side of the valley, with

the Columbia Mountains to the southwest. Goats were monitored up to 28 km from the main valley. Elevations ranged from 715 m at the northwest end of the valley bottom to surrounding peaks that were generally between 2600 and 3250 m. Shackleton (1999) rated the relative density of goats in the area as moderate. Within a 2700-km^2 census zone (above 1675 m) encompassing the study animals, the goat density was estimated at 0.8 goats/km^2 (Poole et al. 2000).

Climate varied with elevation, with a general increase in precipitation and decline in temperature with increasing elevation. Mean July and January temperatures for Valemount, located at 797 m in the centre of the study area, were 15.8 and –11.0°C, respectively, with an average annual precipitation of 503 mm, 180 mm of which fall as snow (Environment Canada climate normals, unpublished data). At elevations the goats frequented, snow cover was usually present from about late September to early June. Snow water equivalent data (snow pillow; BC MELP, unpublished data) from monitoring stations at the north (at 1690 m elevation) and south (1980 m) ends of the study area indicated that snow depths during winter 1997–1998 were approximately 20% below normal, while in 1998–1999 they were 5–25% greater than normal (both stations n = 13 yr). Spring snow melt in 1998 was about three weeks earlier than normal, while in 1999 it was two to four weeks later than normal.

Four biogeoclimatic zones were represented in the study area, ranging from the sub-boreal spruce (SBS) and interior cedar-hemlock (ICH) zones in the valley bottom, through the Engelmann Spruce-Subalpine Fir (ESSF) zone to the alpine tundra (AT) at the highest elevations (Meidinger and Pojar 1991). Treeline was generally between 1900 and 2150 m. In the valley bottom, hybrid spruce (*Picea glauca* × *engelmannii*), Subalpine Fir (*Abies lasiocarpa*), Western Hemlock (*Tsuga heterophylla*), and Western Redcedar (*Thuja plicata*) were the dominant trees, with extensive stands of Lodgepole Pine (*Pinus contorta*) due to frequent fires (MacKinnon et al. 1992). Higher up the mountainsides spruce, Subalpine Fir and Lodgepole Pine predominated, with scattered stands of Whitebark Pine (*Pinus albicaulis*) at the highest elevations. In the AT zone, conifers were present only in stunted krummholz forms in the lower levels of this zone; much of the zone consists of sparse vegetation, rock, talus, and glaciers or semi-permanent snowfields. Cliff formations vary from sheer faces to broken bluffs.

Potential predators of goats (Côté and Festa-Bianchet 2003) within the study area included Wolves (*Canis lupus*), Grizzly Bears (*Ursus arctos*), Black Bears (*U. americanus*), Cougars (*Puma concolor*), Wolverines (*Gulo gulo*), and Golden Eagles (*Aquila chrysaetos*). The main form of industrial development off the Robson Valley was forestry, and most major and some minor watersheds had logging roads along at least part of the valley bottom. Logging was generally at lower elevations and varied greatly in extent among drainages. Most upper elevations and the back ends of most watersheds were undeveloped wilderness. Goat hunting was permitted throughout the study area through open seasons or limited entry quota, depending upon the area (15 August – 15 October), but was generally very light (≤1% of the population estimate; Poole et al. 2000). Hunters were allowed to shoot one goat/yr of either sex, but were requested to shoot a male.

Methods

Capture and Telemetry

We captured goats with a hand-held net gun fired from a Hughes 500, A-star or Bell 206B helicopter wherever we could find goats in suitable terrain (minimizing risk to the animal), while attempting to distribute the radiocollars throughout the study area and ensure some collars were near drainages where forestry development was imminent. Each animal was hobbled, blindfolded, and fitted with horn guards prior to processing. We aged captured goats by counting the number of distinct horn annuli plus the fainter kid annulus formed at six months of age (Smith 1988; Stevens and Houston 1989). We released captured goats generally within 20 minutes of netting. Goat capture protocols were approved by H. Schwantje, the British Columbia Ministry of Environment, Lands and Parks veterinarian, Victoria, who participated in 10 captures.

VHF radiocollars (model LMRT-3, Lotek Engineering Inc., Newmarket, Ontario) weighed 400 g and were designed to last 35 months. GPS radiocollars (Advanced Telemetry Systems [ATS], Isanta, Minnesota, USA) weighed approximately 950 g and were equipped with a VHF transmitter and a 12-channel Garmin GPS board (Olathe, Kansas, USA). The GPS collars logged non-differentially correctable horizontal position data in the WGS84 datum, altitude, date, time, satellite identifier, location mode (2- or 3-dimensional [2D or 3D]), dilution of precision (DOP), and the time required to obtain a location. The GPS collars operated in auto 2D/3D mode, meaning that when signals from ≥4 satellites were obtained, a 3D location (horizontal position and elevation) was taken, but if only three satellite signals were obtained, a 2D location (horizontal position only) was taken using the elevation obtained from the last 3D location (Rempel et al. 1995). GPS collars were programmed to obtain a GPS location every six hours on the hour (120-second maximum on time with no retry on failed attempts) and had an estimated 181-day GPS battery life (C. Kochanny, Advanced Telemetry Systems, personal communication). One collar collected locations at 0000, 0600, 1200 and 1800 hours, two collars at 0200, 0800, 1400 and 2000 hours, and three collars at 0300, 0900, 1500 and 2100 hours. GPS collars were released from the animals by a remotely fired mechanism (Mech and Gese 1992), collars were picked up, and data from the collar's memory were downloaded through a direct cable connection to a personal computer.

FIGURE 1. Location of the Robson Valley Mountain Goat study, 1997–1999.

We located collared goats using traditional aerial telemetry procedures (Mech 1983; White and Garrott 1990) one to four times monthly using a Cessna 337 with two strut-mounted "H" antennae. Generally, all collared goats were located each flight, although on nine flights poor weather conditions or time restrictions prevented access to every animal. The difficulty of ground access into the study area required that all radiotelemetry monitoring be conducted aerially during daylight hours and good flying weather. During spring and early summer 1998, we often located all goats late in the evening and again early the following morning, to reduce ferry costs per goat location and to maximize the likelihood of locating goats at mineral licks (Singer and Doherty 1985). All other VHF goat locations were ≥4 days apart. At each location we recorded the goat's position using the aircraft's GPS, the vegetation cover and general landscape features and, where possible, group size and composition. All VHF and GPS locations were standardized to Pacific Standard Time.

Accuracy of VHF locations was not tested; however, collared goats were observed on 41% of the 747 locations. Accuracy of GPS locations was also not tested however, non-differentially corrected locations taken before the Selective Availability feature in the US military GPS was removed on 1 May 2000 are expected to be within 100 m of the true location, 95% of the time (Lotek Engineering 1998*). Bowman et al. (2000) found that 84% of GPS locations for ATS collars on White-tailed Deer (*Odocoileus virginianus)* were within 100 m of the actual locations.

To assess the reliability of the location data from the GPS collars, we considered both the accuracy of the individual locations and the potential for bias in the sample of locations. Location accuracy is inversely related to dilution of precision values, and 3D locations have a higher probability of being more accurate than 2D locations (Trimble Navigation Ltd 1994*; British Columbia Ministry of Environment, Lands and Parks 1995*; Johnson 2000). Whenever GPS location success is <100%, then GPS locations likely represent a biased sample of habitat use because location success is affected by factors like tree density, canopy cover and topography (Rempel et al. 1995; Moen et al. 1996; Dussault et al. 1999; D'Eon et al. 2002). This was especially important in our study because we were interested in documenting forest use by goats. To assess this bias we considered both the GPS location success rate and the proportion of 2D fixes among seasons. If tree cover reduced the likelihood of obtaining a location, then 2D forest locations should be relatively more common than 3D forest locations, because the collar must 'see' at least one more satellite for a 3D location.

Spatial Analysis

We imported goat locations into a geographic information system (GIS; ARC/INFO; Environmental Systems Research Institute, Redlands, California, USA) for mapping and spatial analysis, and determination of vegetation cover and topography of goat locations (see below). We divided each year into winter (1 November–15 May), kidding (16 May–15 June), and summer/fall (16 June–31 October). We examined locations and movements of collared goats to identify mineral licks for management planning, both during aerial location flights and subsequently during examination of the GPS location data.

We conducted movement analysis and home range estimation using the Animal Movement extension (Hooge and Eichenlaub 1997*) for ArcView (Environmental Systems Research Institute, Redlands California, USA). We calculated 100% minimum convex polygon (MCP) home range for all goats monitored for >1 year and for calculating seasonal ranges, and removed obvious outliers (i.e., trips to mineral licks) prior to analysis. Seasonal activity centres were calculated using the Spider Diagram option in Animal Movement extension (Hooge and Eichenlaub 1997*) for ArcView.

Habitat Analysis

Using GIS, we plotted goat locations on digital 1:20 000 scale forest inventory planning maps (forest cover; Resources Inventory Branch 1995), and digital 1:20 000 scale topographic Terrain Resource Information Mapping data (TRIM; Surveys and Resource Mapping Branch 1992). We determined the following characteristics of each goat location: elevation, average location aspect (in 90° intervals centred on the four cardinal directions), percent slope, the two leading tree species (where available), stand age (projected to

1997) and crown closure, and whether the area was mapped as currently supporting or could support commercial (potentially merchantable) forest. Aspect, slope and elevation were calculated by creating a triangulated irregular network (TIN) developed from digital elevation models (DEMs), which averaged those parameters over each TIN; TINs were generally 60–100 m on a side. Because goats are reported to be usually within 400 m of steep, rocky terrain (Smith 1986; Haynes 1992), we created a 50-m grid over the study area, assigned a mean slope to each grid cell, and determined the distance from each GPS collar location to potential escape terrain, which we classified as cells with >100% slope. Mapped definitions of escape terrain vary, and range from areas with >47% and ≥65% slope for Colorado goats (Varley 1994; Gross et al. 2002), through >84% slope in coastal British Columbia (Taylor and Brunt 2003*), to >100% slope within the southern Selkirk Mountains of the West Kootenay (Poole and Mowat 1997*). We chose the higher slope to be conservative. We compared distances to escape terrain among seasons using $\log_{10}$ transformed data.

We included VHF locations from both evening and morning telemetry flights in all analyses of VHF-derived data, although we acknowledge that the characteristics of these paired locations were likely correlated. Given the relatively fine-grained environment in which they lived, goats had the opportunity to move among habitat types between flights, even if they did not have time to cross their entire home range. For most analyses, we pooled the VHF locations for all goats throughout the study period, because we had relatively small numbers of locations for a relatively large number of animals (White and Garrott 1990). We compared elevation and slope used among seasons using paired *t*-tests among the means of individual goats, and the distribution of aspects and cover types used among seasons using Chi-squared tests. Using GPS data, we examined the influence of time of day on goat use of elevation and slope, and travel rate for six-hour periods during the day (0030-0630, 0063-1230, 1230-1830, and 1830-0030 hr) using a repeated measures ANOVA and Ryan's multiple range test (SAS Institute Inc. 1997); travel rate data were $\log_{10}$ transformed. Travel rates (m/hr) were obtained only from GPS locations obtained at six-hour intervals. All analyses were performed using SAS (SAS Institute Inc. 1997) or Statistica (StatSoft Inc. 1997) software. Statistical tests were considered significant at $P < 0.05$. Means are presented with associated standard errors (SE), except where noted.

Results

Goat capture and monitoring

We captured and collared 21 goats [15 females (F), 6 males (M)] in three sessions (4 F in late July 1997 and 7 F and 3 M in early September 1997, all with VHF collars; and 3 F and 4 M in early March 1999, 3 F and 3 M with GPS collars, 1 M with a VHF collar). Estimated age of goats at capture ranged from 2–9 years for females ($\bar{x} = 5.1 \pm 0.49$ yr) and 5–11 years for males (7.6 ± 0.90 yr). One female goat captured in September 1997 died within a week of handling, possibly because of capture myopathy, and was removed from all analyses. Two goats died later in the study, both of unknown natural causes. We obtained 747 VHF collared goat locations (10–57 locations/goat) between July 1997 and October 1999, and 3639 GPS locations over a 28-week period from six GPS collars deployed from March to September 1999.

Reliability of the GPS Collar Locations

Three-dimensional locations were obtained on 80% of successful locations, and mean location success rate of GPS collars was 76% (Table 1). Five of the collars functioned much better than the sixth, obtaining locations on 85% of their attempts. Factors other than forest cover appeared to be responsible for many of missed location attempts because, (1) the VHF-collared goats were found in forest 3.5 times more often in winter than from spring through fall (Table 2), but the proportion of GPS location failures increased only slightly among winter, kidding and summer (means of 13%, 13%, and 18%, respectively), and (2) the proportion of 2D locations remained relatively stable among seasons (means of 18%, 19%, and 21%, respectively). The proportion of 2D locations was highest for forest locations (Table 3).

TABLE 1. Success rate of GPS collars programmed to obtain four locations daily, deployed on Mountain Goats in the Robson Valley, British Columbia, March to September 1999.

Goat ID	Days in field	Number of locations	% of expected locations	2D locations (% of total no.)	3D locations (% of total no.)
9917	195	240	31	23	77
9918	195	629	81	28	72
9919	204	703	88	19	81
9920	204	719	86	20	80
9921	204	714	88	6	94
9923	194	634	82	27	73
Weighted mean	199	607	76	20	80

TABLE 2. Distribution (%) of forest cover descriptors in polygons containing VHF locations for 21 Mountain Goats, July 1997 to October 1999, and GPS locations from six goats, March to September 1999, Robson Valley, British Columbia. Winter covers 1 November to 15 May.

Collar type	Season	*n*	Alpine	Alpine forest	Commercial forest	Other[a]
VHF	Winter	287	59	9	26	7
	Spring to fall	460	84	4	7	5
GPS	Late winter	1324	75	6	9	10
	Spring to late summer	2315	86	2	7	6

[a] Other included clearings, clay banks, rock, non-productive brush and burns, and non sufficiently restocked areas.

TABLE 3. Percent of 2D and 3D locations from GPS radio collars within broad vegetation cover types (defined by biogeoclimatic zone and forest cover mapping) from Mountain Goats in the Robson Valley, British Columbia, March to September 1999.

Location type	Biogeoclimatic zone[a]		Forest cover[b]		
	Alpine tundra	ESSF[c]	Alpine	Alpine forest	Forest
n	2984	655	3005	367	267
2D	18	28[d]	18	27	36
3D	82	72	83	73	64

[a] $\chi^2_1 = 1830$, $P < 0.0001$.
[b] $\chi^2_2 = 1680$, $P < 0.0001$.
[c] ESSF = Engelmann Spruce – Subalpine Fir biogeoclimatic zone.
[d] Includes one location in ICH (Interior Cedar Hemlock).

Although we can never know where the goats were when the collars failed to obtain a location, we used data from the five GPS collars that had no obvious technical malfunctions (i.e., excluding goat 9917) to assess the magnitude of any bias against forest locations. If location success was reduced when goats were in the forest and if goats tended to remain in the forest for >1 location attempt, then missed location attempts should be more common following a forest location than following an alpine location. For all five collars, forest locations were far more likely than non-forest locations to be followed by a forest location (means of 53% versus 7%, respectively) but missed locations were only slightly more common following forest locations (mean of 20% versus 16%, respectively). We inferred from these data that the magnitude of the bias against obtaining a forest location was about 23% (the ratio of the proportion of forested zones in the location subsequent to a missed location compared to a successful location; 20.1%/16.3%).

Population Scale Movements

As expected, all goats used steep terrain and were found at lower elevations during winter. The goats monitored for >1 year followed one of two seasonal movement patterns. Eight of 11 goats occupied relatively small (12–17 km^2) home ranges with primarily seasonal shifts in elevation, while three exhibited longer horizontal shifts, moving 8–13 km between seasonal activity centres. Only two collared goats could be considered as belonging to the same herd; both these animals made primarily elevational shifts in range use. Movement to wintering areas usually occurred between early October and late November, with an initial drop to lower elevations followed by a slight increase in elevation during December (Figure 2). Only two male goats were monitored during the first winter, and both wintered at low elevations (Figure 2). Both VHF and GPS data suggested that initial movements to lower elevations coincided with the first fall snowstorm. The two adult female goats wearing GPS collars in late September descended roughly 500 m in elevation during and just after the winter's first snowstorm on 24–25 September, while the only male still with a GPS collar at that time descended about 100 m. Movement to higher elevation summer range generally took place during June and July. Most goats (8 out of 12) wintered in the same area both winters, but three females and one male shifted wintering areas between years. Mean home range size (100% MCP) of female goats was 27.0 km^2 (±8.50; $n = 10$, range = 6–98 km^2). The two males had home ranges of 13.7 and 65.3 km^2. Goats tended to move very little over winter. Mean movement rates of the five goats carrying functioning GPS collars ranged from 24–36 m/h in winter and from 60–115 m/h during summer, with winter range size often very small. One female used areas of about 15 and 35 ha located 1.5 km apart in successive winters, and one male wintered both years in the same 72 ha area.

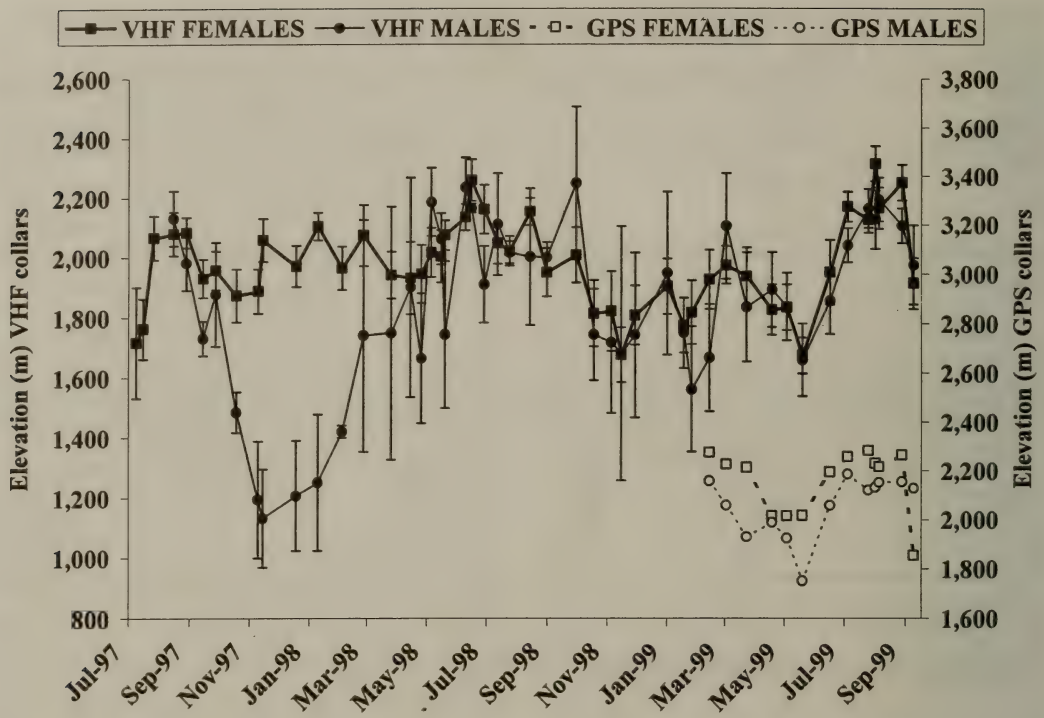


FIGURE 2. Mean elevation (m ± SE) of female and male VHF-collared Mountain Goats (solid lines and left axis) plotted by telemetry flight, September 1997 – October 1999, and male and female GPS-collared Mountain Goats (dashed lines and right axis), March – September 1999, Robson Valley, British Columbia. The right axis was offset to show the GPS collars separately. VHF sample sizes were 6–13 for females and 2–6 for males (only two males were monitored the first winter); GPS sample sizes were three male and three female goats.

Habitat Use

Goats used lower elevations during winter (1 November – 15 May; $\bar{x}$ = 1730 ± 59 m; n = 12) compared with the rest of the year ($\bar{x}$ = 1920 ± 43 m; n = 12; t_{11} = 3.9, P = 0.0024; Figure 2). Ninety percent of winter goat locations were between 1330 and 2320 m in elevation (n = 287). Mean annual slope use among goats monitored >1 year averaged 79% (± 2.1%). Goats occupied slopes of similar steepness in winter as they did during the rest of the year (t_{11} = 1.0, P = 0.35). GPS-collared goats were closer to escape terrain during late winter than during the snow-free periods (n = 5; t = 2.03, P = 0.04) with use declining with increasing distance from escape terrain, especially beyond 500 m (Figure 3). Seventy percent of locations during winter and 62% during summer were <500 m from escape terrain.

Southern aspects were used more often (44% of locations) throughout the year by VHF-collared goats than were other aspects, and east and west aspects were used less often than would be expected from a random distribution (χ^2_3 = 410, P < 0.0001). Goats were located 15% more often on south aspects during winter than from spring to fall (χ^2_3 = 45.6, P < 0.0001).

Over the year, 70% of VHF locations of goats were found in the AT biogeoclimatic zone, 29% were in the ESSFmm1 (moist, mild) subzone/variant; and 1.2% (9 locations) were found in the ICH zone. Overall, 14% of VHF goat locations were in forest cover polygons mapped as commercial forest and most locations were in the alpine (Table 3). Seven percent of GPS locations were in commercial forest. Use of alpine areas increased between winter and snow-free seasons for both VHF-collared goats monitored over the entire year, and GPS-collared goats monitored from March to September; use of commercial forests by VHF-collared goats increased to 26% during winter (VHF: χ^2_3 = 66.6, P < 0.0001; GPS: χ^2_3 = 89.7, P < 0.0001; Table 3). As summer progressed all GPS-collared animals were found almost exclusively in the alpine, including 98% of all locations after 12 July.

Subalpine Fir, spruce, and Lodgepole Pine were the leading tree species (64–71% of the total gross volume of each stand) in commercial forest stands where collared goats were located, and spruce, Subalpine Fir, Lodgepole Pine and Whitebark Pine were most prevalent as the second species (23–25% of volume; Table 4). Trees in alpine forest polygons were prima-

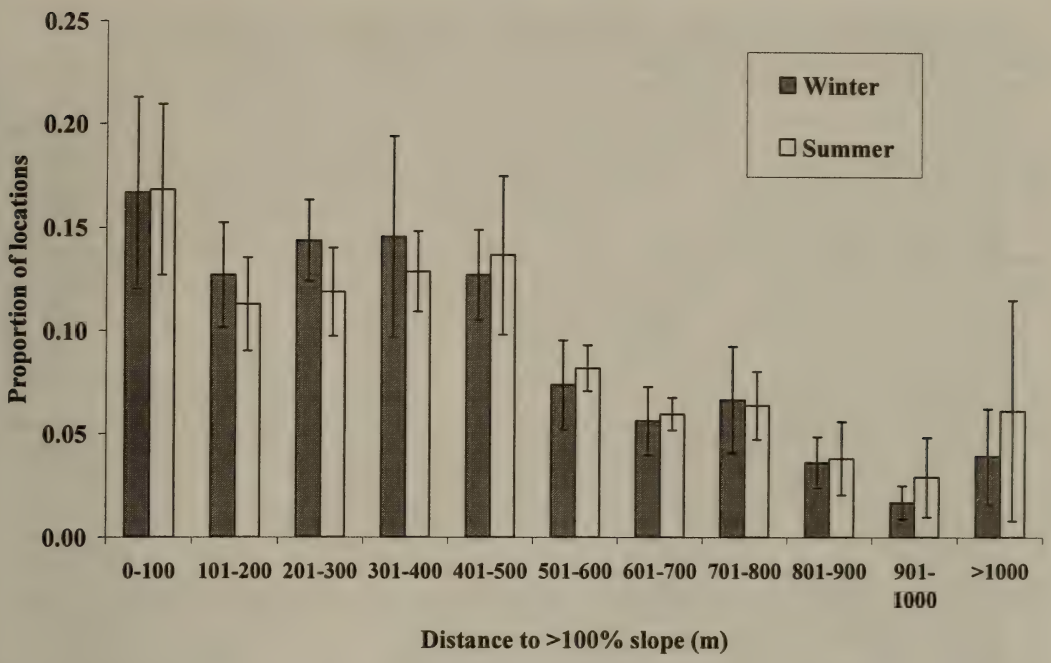


FIGURE 3. Proportion of GPS collared goat locations (±SE) in relation to distance from escape terrain (areas of >100% slope) for six Mountain Goats, Robson Valley, March – September 1999. Winter covers the period from early March to 31 May; summer from 1 June to late September.

rily Subalpine Fir or a mix of Subalpine Fir and spruce. Ninety-eight per cent of commercial forest stands (n = 372) were mature (81–140 years; 25%) or old (>140 years; 73%), while only 2% were immature (21–80 years). Subalpine Fir and spruce dominated old stands. All but six alpine forest stands were mature or old in age (n = 155). Crown closure of stands used during winter ranged from 5 to 65%, with 79% of goat use in stands with between 26 and 45% crown closure.

Using GPS collar data, the period of the day appeared to affect elevation used and movement rates but not slope or aspect. The goats were found on average 50 to 70 m lower in elevation from evening to dawn (1830–0630 hr) compared with the rest of the day and movement rates were lower during the period from 0030 to 0630 h (Table 5). There was no difference among periods of the day in aspect selected (χ^2_9 = 14.1, P = 0.12) or in the use of broad forest cover type (χ^2_9 = 7.9, P = 0.54).

Mineral Licks

Local residents told us of the location of 16 goat mineral licks that were primarily from low and mid-elevations in the northern half of the study area (G. Calef and D. Heard, unpublished data). Three of the VHF-collared goats spent time at or near three of these mid-elevation licks during the study. We located three new mineral licks or focal areas (areas which we assumed contained licks because goats seemed to concentrate their activity there in the same way they did at known mineral licks, but where we could not find a specific lick site), all at upper elevations (2000–2300 m) and all in the alpine zone in the southern portion of the study area. Six collared goats visited these licks. One of the areas was within a goat's home range, and two were located 6–14 km outside of normal home ranges (Figure 4). GPS collar locations suggested visits to the sites lasted from <24 h to four days. Visits to all licks or focal areas occurred from March through November, with most use of high-elevation sites between June and September.

Discussion

Movements and Habitat Use

As expected, at the population scale goats in the Robson Valley generally used high, steep terrain. The goats spent up to 26% of the winter in potentially merchantable timber stands when they were not using low-snow areas near or above treeline. Those seasonal movements and habitat use were similar to goats occupying other dry interior regions (Smith 1977; Adams and Bailey 1983). Goats living in coastal and wet interior climates, where winter snow fall is much greater, typically spend more time in forests (e.g., over 85% of winter goat locations in coastal Alaska occurred in forests [Smith 1986]) presumably because goats prefer the lower snow depths found under trees

TABLE 4. Distribution (%) of the first and second leading commercial tree species (by gross volume) in forest cover polygons containing VHF locations for Mountain Goats, July 1997 – March 1999, and GPS locations from six goats, March to September 1999, Robson Valley, British Columbia.

Collar type		*n*	Subalpine Fir	Spruce	Lodgepole Pine	Douglas-Fir	Whitebark Pine	Other[a]
VHF	Leading	105	39	25	18	7	5	7
VHF	Second	104	33	30	16	4	13	4
GPS	Leading	417	77	13	1	0	9	0
GPS	Second	406	18	32	18	0	32	0

[a] Other includes aspen (*Populus tremuloides*), Paper Birch (*Betula papyrifera*), Western Redcedar, and Western Hemlock.

TABLE 5. Elevation, slope, and travel rate for six GPS-collared Mountain Goats by six-hour periods, Robson Valley, March–September 1999.

Period (hr)	*n*	Elevation (m)[a] $\bar{x}$	SE	Slope (%)[b] $\bar{x}$	SE	Travel rate (m/hr)[c] $\bar{x}$	SE
0030–0630	898	2060B[d]	8	78	0.9	35B	1.7
0630–1230	918	2130A	8	78	1.0	68A	3.9
1230–1830	891	2130A	8	77	1.0	64A	3.0
1830–0030	926	2080B	8	77	1.0	67A	3.3

[a] $F_{3,5} = 16.5$, $P < 0.0001$
[b] $F_{3,5} = 0.7$, $P = 0.55$
[c] $F_{3,5} = 35.4$, $P < 0.0001$ ($\log_{10}$ transformed data)
[d] Means within a column with the same letter did not differ.

(Smith 1977; Hebert and Turnbull 1977; McCrory et al. 1977; Adams and Bailey 1983; Fox and Smith 1988; Gilbert and Raedeke 1992). Robson Valley goats wintered in forests primarily composed of open mature or old-aged Subalpine Fir and spruce stands at the upper reaches of continuously forested slopes. While mapped as potential commercial forest in the forest cover database, most of these stands were located on steep terrain and were interspersed with or adjacent to small to medium-sized (5–20 m) cliffs that would not be mapped in the forest cover database (K. Poole and D. Heard, personal observations). While those stands could have forestry development potential, over the short to medium term their economic value is low compared to stands at lower elevation and on less steep and broken slopes.

We observed changes in elevation that were probably related to snow conditions and food availability. Goats moved lower with the first heavy winter snowfall and with the onset of the spring vegetation green-up. Goats moved up through late spring and summer, likely, as suggested by Varley (1994), coinciding with greening up of vegetation and snow melt at progressively higher elevations. Areas used over winter before the firming of the snow crust in late winter were often very small.

Seasonal movement patterns varied from short shifts up and down a mountain face, to movements among distant areas. Those differences in movement patterns account for the large differences in home range size among individuals. Overall both the mean and the variation among home range size of female goats in the Robson Valley was similar to published 100% MCP home range sizes of female goats' range from other areas (means among studies of 8.9–25.0 km^2 for females; Rideout 1978; Singer and Doherty 1985; Côté and Festa-Bianchet 2003).

Focal Areas and Mineral Licks

Prior to this study, most of the known goat mineral licks in the Robson Valley were typical seeps or cut banks (Hebert and Cowan 1971), and in forested valley bottoms where people would be most likely to find them. During this study we were able to identify three new high elevation mineral licks or focal areas. High elevation licks have also been reported near edges of glaciers, glacier moraines, caves, limestone outcrops, and shale cliffs elsewhere in British Columbia (McCrory 1979*). We could have missed movements of VHF collared goats to mineral licks, but because of the high location success of the GPS collars and the relatively low bias against forest locations, we believe it unlikely that we failed to detect use of other licks outside of their normal home ranges. The comparatively low incidence of long-distant movements by GPS-collared goats suggests that sources of minerals may be more widespread in the Robson Valley than elsewhere. While prevalent in most goat populations,

FIGURE 4. Locations and movements of adult female Mountain Goat 9919 in the Robson Valley, British Columbia, 9 March to 29 September 1999, based on locations determined by the GPS receiver in the radio-collar (n = 703, open circles) and by tracking the VHF signal from the radio-collar (n = 11, dots within circles). Line joins the eight consecutive GPS location points from 17 and 18 August 1999 where the Mountain goat was found during a movement to a focal area outside of her normal home range. Dark stippled areas represent glaciers.

use of mineral licks by goat populations is not universal (Varley 1994) and there is a great deal of individual variation among goats in the number of lick visits, timing and duration of visits, and distance traveled to licks (Hebert and Cowan 1971; Singer and Doherty 1985; Hopkins et al. 1992; Klaus and Schmid 1998; Lemke 1999*). Our observations were consistent with the generalization that peak use of licks varies with elevation, with higher elevation licks being used later in the season (Hebert and Cowan 1971).

GPS Technology

GPS collars can provide numerous precise locations, but because location success is always <100% the recorded positions are undoubtedly biased. Location success is related to differences in overstory vegetation (Rempel et al. 1995; Moen et al. 1996; Dussault et al. 1999; D'Eon et al. 2002), topography (D'Eon et al. 2002), and animal behaviour (Edenius 1997; Bowman et al. 2000; Moen et al. 2001). The GPS locations likely underestimated the use of forest stands with higher crown closures and stem densities. Quantifying this bias is difficult, but we suggest that forest use may be underestimated by about 23% because VHF collar data suggested higher use of commercial forests by goats during winter than the GPS collar data. However, forest use during late winter (when the GPS collars were deployed) and the firming of snow conditions may be less than found during other periods of the winter. This study was not a good test of the impact of canopy closure on GPS location success, because even when located in an area mapped as "forest", goats may have been on small cliffs with little or no adjacent tall vegetation, and not in stands with continuous crown closure. Our data suggests that factors other than vegetation cover density were also responsible for

many of the missed location attempts because collar acquisition success did not differ between summer, when it was highly unlikely that goats were ever in forests, and other seasons. It may be possible to define correction factors better using field trials, or increased spatial modeling and examination using GIS (e.g., D'Eon et al. 2002).

Most studies of bias in GPS location success have been conducted in relatively flat terrain in central and eastern North America, and the results from studies in mountainous terrain provide conflicting results as to the impact of topography (Dussault et al. 1999; D'Eon et al. 2002). The 76% location success rate in this study was at the upper end of the range reported elsewhere (Johnson et al. 2002). GPS collars may be particularly appropriate for studies on goats and other animals living in rugged, non-forested or lightly forested terrain, or when detection of short-term movements outside of an animal's normal home range is required.

The GPS collar data suggested that goats conducted movements to lower elevations during the evening to dawn period. This finding suggests that VHF-based locations on goats and possibly other species may be biased where safety and logistics dictate that animal locations be taken during daylight hours and in good weather, e.g., when telemetry locations are required from aircraft.

Management Implications

The absence of detected goat movements to low-elevation sites and limited movements to areas outside of their normal home ranges suggests that the minerals sought by goats in the Robson Valley during spring and summer may be widely available. This would further suggest that goats in the Robson Valley may face less risk to disturbance from forestry development at mineral licks, since few appear to use low elevation licks.

Robson Valley goats also appeared to be at relatively low risk from logging on their winter range. While we demonstrated that goats in the Robson Valley use forests, primarily during winter, most of these stands were on steep slopes in association with scattered, non-forested cliffs at the upper edge of continuous forested habitats. The timber in these areas appeared to be of low commercial value over at least the short to medium term. Forest development planning can incorporate low elevation forest and mineral lick use by goats by avoiding development adjacent to cliffs located in forested habitats. The reported distance from escape terrain within which goats are most often found varies from 260–500 m (Fox 1983; Smith 1994; Poole and Mowat 1997*; Gross et al. 2002). In the Robson Valley, a forested buffer of 500 m around cliffs should be left to reduce the possibility of adverse effects on goats; these buffers should be especially enforced around cliffs on southern aspects and at elevations down to about 1300 m.

Acknowledgments

Funding was provided by Forest Renewal British Columbia, Resources Inventory Program, and was administered by British Columbia Ministry of Environment, Lands and Parks (MELP), Prince George, British Columbia. G. Watts, J. Hooge, C. Leake, H. Schwantje, and M. Badry provided field and study assistance, G. Calef summarized mineral lick use by goats in the region, and W. Poole provided rock identification. C. Ritchie, MELP, Prince George, provided input on forestry development in the region. C. Wilson, B. Scott, B. Minor, G. Altoft, and G. Watts captured the goats, and B. McPherson, D. Brady, and C. Blunt provided additional helicopter support. D. Mair provided excellent and enthusiastic piloting for telemetry flights. We thank C. Kochanny and N. Christensen at ATS, Isanti, Minnesota, for technical support during the project. D. Pritchard conducted the GIS analyses. G. Mowat, M. Festa-Bianchet, and two anonymous reviewers commented on earlier drafts of the manuscript. Mention of brand names or commercial products is solely for the purpose of description and does not imply endorsement by the authors or affiliated agencies.

Documents Cited (marked * after year in text)

British Columbia Ministry of Environment, Lands and Parks. 1995. British Columbia standards, specifications and guidelines for resource surveys using global positioning system (GPS) technology. Ministry of Environment, Lands and Parks, Surveys and Resource Mapping Branch, Victoria, British Columbia, Canada.

Hooge, P. N., and **B. Eichenlaub.** 1997. Animal movement extension to ArcView. Version 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska, USA.

Lemke, S. L. 1999. Cayoosh Range mountain goat study results and recommendations. Unpublished report for BC Ministry of Environment, Lands and Parks, Kamloops, British Columbia, Canada.

Lotek Engineering. 1998. N3WIN Differential Post-processing Software User's Manual (Release 2.40: January 1998). Lotek Engineering, Newmarket, Ontario, Canada.

McCrory, W. P. 1979. An inventory of the mountain goats of Glacier and Mount Revelstoke National Parks, British Columbia. Unpublished report. Parks Canada, Western Region, Glacier National Park, Revelstoke, British Columbia, Canada.

Poole, K. G., and **G. Mowat.** 1997. Mountain goat winter habitat use in the West Kootenay Region of British Columbia. Unpublished report for B.C. Ministry of Environment, Lands and Parks, Nelson, British Columbia.

Taylor, S. D., and **K. Brunt.** 2003. Winter habitat use by mountain goats in the Kingcome River drainage of coastal British Columbia. Unpublished report for B.C. Ministry of Water, Land and Air Protection, Naniamo.

Trimble Navigation Ltd. 1994. Mapping systems: general reference. Trimble Navigation Ltd., Sunnyvale, California, USA.

Literature Cited

Adams, L. A., and **J. A. Bailey.** 1983. Winter forages of mountain goats in central Colorado. Journal of Wildlife Management 47: 1237–1243.

Bowman, J. L., C. O. Kochanny, S. Demarais, and **B. D. Leopold.** 2000. Evaluation of a GPS collar for white-tailed deer. Wildlife Society Bulletin 28: 141–145.

Côté, S. D., and **M. Festa-Bianchet.** 2003. Mountain goat. Pages 1061–1075 *in* Wild mammals of North America: biology, management, and conservation. *Edited by* G. A. Feldhamer, B. Thompson, and J. Chapman. The John Hopkins University Press, Baltimore, Maryland.

Demarchi, M. W., S. R. Johnson, and **G. F. Searing.** 2000. Distribution and abundance of mountain goats, *Oreamnos americanus*, in westcentral British Columbia. Canadian Field-Naturalist 114: 301–306

D'Eon, R. G., R. Serrouya, G. Smith, and **C. O. Kochanny.** 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin 30: 430–439.

Dussault, C., R. Courtois, J.-P. Ouellet, and **J. Huot.** 1999. Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. Wildlife Society Bulletin 27: 965–972.

Edenius, L. 1997. Field test of a GPS location system for moose *Alces alces* under Scandinavian boreal conditions. Wildlife Biology 3: 39–43.

Fox, J. L. 1983. Constraints on winter habitat selection by the mountain goat, *Oreamnos americanus*, in Alaska. Ph.D. dissertation, University of Washington, Seattle.

Fox, J. L., and **C.A. Smith.** 1988. Winter mountain goat diets in southeast Alaska. Journal of Wildlife Management 52: 362–365.

Gilbert, B. A., and **K. J. Raedeke**. 1992. Winter habitat selection of mountain goats in the North Tolt and Mine Creek drainages of the North Central Cascades. Biennial Symposium of the Northern Wild Sheep and Goat Council 8: 305–324.

Gross, J. E., M. C. Kneeland, D. F. Reed, and **R. M. Reich**. 2002. GIS-based habitat models for mountain goats. Journal of Mammalogy 83: 218–228.

Haynes, L. A. 1992. Mountain goat habitat of Wyoming's Beartooth Plateau: implications for management. Biennial Symposium of the Northern Wild Sheep and Goat Council 8: 325–339.

Hebert, D., and **I. M. Cowan.** 1971. Natural salt licks as a part of the ecology of the mountain goat. Canadian Journal of Zoology 49: 605–610.

Hebert, D., and **W. G. Turnbull.** 1977. A description of southern interior and coastal mountain goat ecotypes in British Columbia. Pages 126–146 *in* Proceedings of the First International Mountain Goat Symposium, Kalispell, Montana. *Edited by* W. M. Samuel and W. G. Macgregor. British Columbia Fish and Wildlife Branch, Victoria, British Columbia, Canada.

Hopkins, A., J. P. Fitzgerald, A. Chappell, and **G. Byrne.** 1992. Population dynamics and behavior of mountain goats using Elliot Ridge, Gore Range, Colorado. Biennial Symposium of the Northern Wild Sheep and Goat Council 8: 340–356.

Johnson, C. J. 2000. A multi-scale behavioural approach to understanding the movements of woodland caribou. Ph.D. thesis, The University of Northern British Columbia, Prince George, British Columbia, Canada.

Johnson, C. J., D. C. Heard, and **K. L. Parker.** 2002. Expectations and realities of GPS animal location collars: results of three years in the field. Wildlife Biology 8: 153-159.

Klaus, G., and **B. Schmid.** 1998. Geophagy at natural licks and mammal ecology: a review. Mammalia 62: 481-497.

McCrory, W. P., D. A. Blood, D. Portman, and **D. Harwood.** 1977. Mountain goat surveys in Yoho National Park, British Columbia. Pages 69–73 *in* Proceedings of the First International Mountain Goat Symposium, Kalispell, Montana. *Edited by* W. M. Samuel and W. G. Macgregor. British Columbia Fish and Wildlife Branch, Victoria, British Columbia, Canada.

MacKinnon, A., J. Pojar, and **R. Coupé.** *Editors*. 1992. Plants of northern British Columbia. Lone Pine Publishing, Vancouver, British Columbia, Canada.

Mech, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis, Minnesota, USA.

Mech, L. D., and **E. M. Gese.** 1992. Field testing the Wildlink capture collar on wolves. Wildlife Society Bulletin 20: 249–256.

Meidinger, D., and **J. Pojar.** 1991. Ecosystems of British Columbia. Special Report Series 6, British Columbia Ministry of Forests, Research Branch, Victoria, British Columbia, Canada.

Moen, R., J. Pastor, Y. Cohen, and **C. C. Schwartz.** 1996. Effects of moose movement and habitat use on GPS collar performance. Journal of Wildlife Management 60: 659–668.

Moen, R., J. Pastor, and **Y. Cohen.** 2001. Effects of animal activity on GPS telemetry location attempts. Alces 37: 207–216.

Poole, K. G., and **D. C. Heard.** 1998. Habitat use and movements of mountain goats as determined by prototype GPS collars, Robson Valley. British Columbia. Biennial Symposium of the Northern Wild Sheep and Goat Council 11: 22–35.

Poole, K. G., D. C. Heard, and **G. S. Watts.** 2000. Mountain goat inventory in the Robson Valley, British Columbia. Biennial Symposium of the Northern Wild Sheep and Goat Council 12:114-124.

Rempel, R. S., A. R. Rodgers, and **K. F. Abraham.** 1995. Performance of a GPS animal location system under boreal forest canopy. Journal of Wildlife Management 59: 543–551.

Resources Inventory Branch. 1995. Relational data dictionary (RDD) 2.0. British Columbia Ministry of Forests, Victoria.

Rideout, C. B. 1978. Mountain goat. Pages 149–159 *in* Big game of North America – ecology and management. *Edited by* J. L. Schmidt and D. L. Gilbert. Wildlife Management Institute, Stackpole Books, Harrisburg, Pennsylvania, USA.

SAS Institute. 1997. SAS/STAT software: changes and enhancements through release 6.12. SAS Institute, Cary, North Carolina, USA.

Shackleton, D. 1999. Hoofed mammals of British Columbia. The Mammals of British Columbia, Volume 3, Royal British Columbia Museum. UBC Press, Vancouver.

Singer, F. J., and **J. L. Doherty.** 1985. Movements and habitat use in an unhunted population of mountain goats, *Oreamnos americanus*. Canadian Field-Naturalist 99: 205–217.

Smith, B. L. 1977. Influence of snow condition on winter distribution, habitat use, and group size of mountain goats. Pages 174–189 *in* Proceedings of the First International Mountain Goat Symposium, Kalispell, Montana. *Edited by*

W. M. Samuel and W. G. Macgregor. British Columbia Fish and Wildlife Branch, Victoria, British Columbia, Canada.

Smith, B. L. 1988. Criteria for determining age and sex of American mountain goats in the field. Journal of Mammalogy 69: 395–402.

Smith, C. A. 1986. Habitat use by mountain goats in southeastern Alaska. Final Report, Project W-22-1, -2, and -3. Alaska Department of Fish and Game, Juneau, Alaska, USA.

Smith, C. A. 1994. Evaluation of a multivariate model of mountain goat winter habitat selection. Biennial Symposium of the Northern Wild Sheep and Goat Council 9: 159–165.

Statsoft Inc. 1997. STATISTICA for Windows. Release 5.1. StatSoft, Tulsa, Oklahoma, USA

Stevens, V., and **D. B. Houston.** 1989. Reliability of age determination of mountain goats. Wildlife Society Bulletin 17: 72–74.

Surveys and Resource Mapping Branch. 1992. Digital baseline mapping at 1:20,000. British Columbia specifications and guidelines for geomatics. Content Series Volume 3. Release 2.0. British Columbia Ministry of Environment, Lands and Parks, Victoria, British Columbia, Canada.

Varley, N. C. 1994. Summer-fall habitat use and fall diets of mountain goats and bighorn sheep in the Absaroka Range, Montana. Biennial Symposium of the Northern Wild Sheep and Goat Council 9: 131–138.

White, G. C., and **R. A. Garrott.** 1990. Analysis of wildlife radio-tracking data. Academic Press, Toronto, Ontario, Canada.

Received 17 December 2001
Accepted 20 April 2004

Planispiral Burrows from a Recent Lacustrine Beach, Gander Lake, Newfoundland

ROBERT B. MACNAUGHTON

Geological Survey of Canada, 3303 – 33 Street NW, Calgary, Alberta T2L 2A7 Canada; e-mail: romacnau@NRCan.gc.ca

MacNaughton, Robert B. 2003. Planispiral burrows from a Recent lacustrine beach, Gander Lake Newfoundland. Canadian Field-Naturalist 117(4): 577-581.

Simple horizontal, planispiral burrows occur in Recent beach sediments on the south shore of Gander Lake, Newfoundland. The burrows apparently represent deposit feeding, possibly by an arthropod. This occurrence extends the known environmental range of such traces into lacustrine settings and illustrates that such behaviour is not exclusive to marine settings.

Key Words: ichnology, lacustrine, Recent, palaeoecology, Newfoundland.

Ichnology is the study of the physical records of behaviour, including, for example, tracks, trails, burrows, and borings (Bromley 1990). Studies are undertaken both in fossil and Recent contexts (palichnology and neoichnology, respectively). Fossilised traces are referred to as "trace fossils" or "ichnofossils" and are classified using Linnean binominal nomenclature. Although much ichnological research is focused on the fossil record, neoichnology can provide crucial data when interpreting ancient behaviours (e.g., Schäfer 1972; Chamberlain 1975; Ratcliffe and Fagerstrom 1980; Metz 1987).

With the development of ichnology as a science has come the awareness that trace fossils are strongly influenced by environmental limiting factors and that, as a result, assemblages of trace fossils are potent palaeoecological and palaeoenvironmental tools (Frey et al. 1990). However, individual ichnotaxa can occur in a broad spectrum of depositional settings. This note reports an occurrence of horizontal, planispiral burrows in Recent beach sediments on the shore of Gander Lake, Newfoundland (Figure 1). Although such traces have been reported from a number of Recent and ancient depositional settings (see below), they are still widely considered to be essentially of marine (especially deep-marine) origin and have been used as a line of evidence for marine deposition (e.g., Mason et al. 1983). This contribution describes the burrows, deduces their probable ethology, and comments on their palaeoecological significance.

Physical Setting

The burrows were observed on the surface of a beach on the south shore of Gander Lake, Newfoundland, Canada. Gander Lake is an elongate, inland body of fresh water with no marine influence. The lake is 47 km long with an average width of 1.9 km and a surface area of 11500 ha (Batterson and Vatcher 1991). The lake's surface elevation is 25 m above sea level and depth soundings of at least 249 m below sea level have been reported (Jenness 1960).

The beach on which the burrows were observed is approximately 90 m east of the mouth of Fifteen Mile Brook (Figure 1). At the time of study, the beach was approximately 3 m wide by 24 m long. It passed on the landward side into forest-covered glacio-fluvial sand and gravel (Figure 1), from which it was probably, in part, derived (cf., Batterson and Vatcher 1991). Small driftwood logs were scattered over the beach. The beach surface consisted of damp to wet (but not water-saturated), muddy to silty, fine- to medium-grained sand containing local concentrations of finely comminuted organic detritus. Grain-size distribution varied over a few tens of centimetres or less, with some areas dominated by silty, fine-grained sand and others by fine- to medium-grained sand. The burrows occurred in both grain-size settings.

Description of Burrows

Four horizontal, planispiral burrows were observed (Figure 2), preserved as positive features on the beach surface. No producer was recovered. The diameter of the spirals ranged from 4 to 6 cm while burrow diameters ranged from 2 to 3 mm. Relief above the beach surface was approximately 1 mm. The burrows were irregularly annulate along their length and contained an apparently structureless fill. Two of the burrows (Figure 2A, B) displayed tight central coils that became progressively more open outward, while the other burrows (Figure 2B) remained tightly coiled. The burrows that became less tightly coiled outward (Figure 2A,B) also differed from the tightly coiled forms in being more regularly coiled. In both types of burrows the central termination was unclear, but was raised slightly above the rest of the burrow. There was no evidence that the sediment surface had been broken at the central termination. One each of the tightly coiled and open-coiled burrows displayed dextral coiling, while the others showed sinistral coiling. In terms of comparisons with the palichnological record, the burrows, especially the regularly coiled examples, show some morphological affinity with *Spirodesmos archi-*

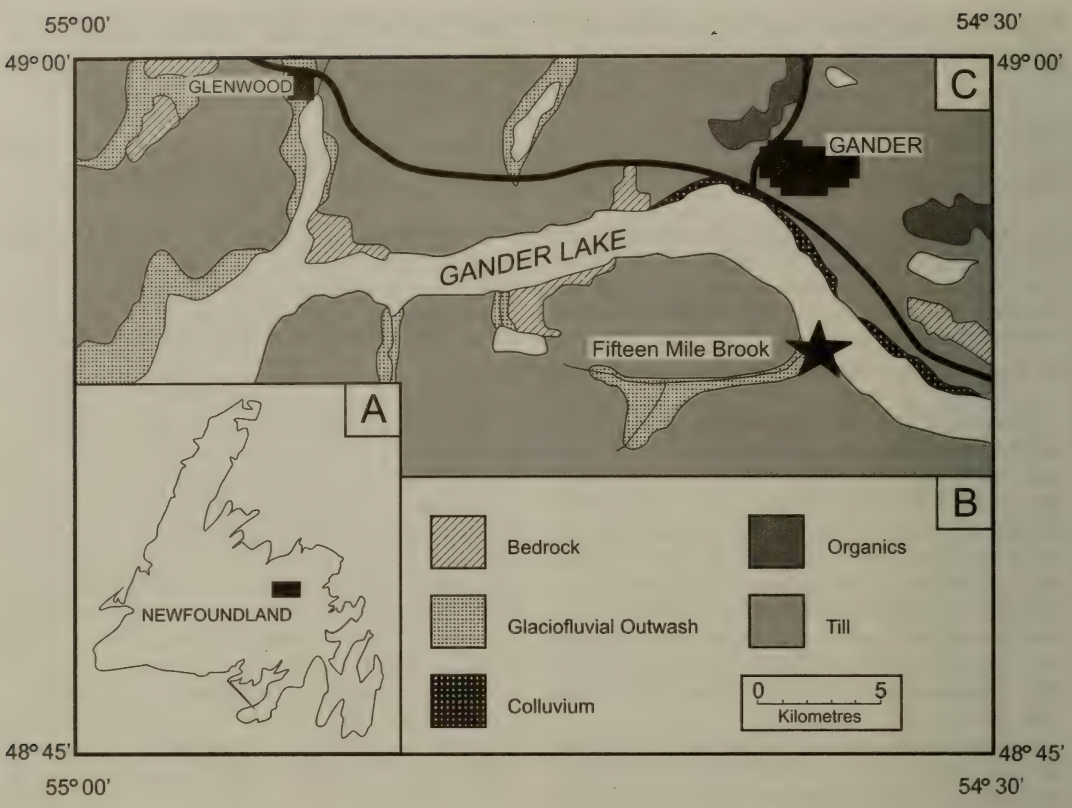


FIGURE 1: Location map. (A) Sketch map of province of Newfoundland. Black box shows location of study area. (B) Legend for main location map. (C) Map showing Quaternary geology of the study area (after Batterson and Vatcher, 1991) and the location of the burrow occurrence on the south shore of Gander Lake (star).

medeus (Huckriede 1952), although *Spirodesmos* does not typically have a raised central area. It should also be noted that there is some question as to whether *Spirodesmos archimedeus* properly belongs within *Spirodesmos*, the type species of which, *Spirodesmos interruptus*, consists of short, individual segments arranged in a planispiral form (Häntzschel 1975).

One burrow (Figure 2B) continued outward as a simple, irregularly turning, horizontal burrow. Two other specimens may have done so prior to weathering, as the outer termination of the spirals pointed toward adjacent, partially weathered, horizontal burrows.

The beach surface also displayed several other types of biogenic structures. These included simple horizontal burrows in positive relief (comparable to *Planolites* in the fossil record), as well as branching horizontal burrows (Figure 2B) and randomly self-crossing horizontal burrows in positive relief (comparable to *Gordia* or *Helminthoidichnites*). Less common traces included bilobate, positive-relief trails (similar to *Aulichnites*), poorly preserved zig-zagging traces (comparable to *Plangtichnus*, but see Buatois and Mángano 1993, on the status of this ichnogenus), and poorly preserved strings of pellets. Tracks of Moose (*Alces alces*) and various birds were also present.

Interpretation of Behaviour

Although it was not possible to recover the producer of these burrows or to observe it producing them, it is nonetheless possible to discuss the burrows' probable ethologic significance. Although planispiral burrows can reflect a number of behaviours, most can be discounted in this case. Mucous-soaked networks of tightly-coiled spiral burrows produced in intertidal flats by the paraonid polychaete, *Paraonis fulgens* (Röder 1971; Schäfer 1972; Risk and Tunnicliffe 1978), serve to trap migrating benthic diatoms, which are then devoured (Röder 1971). However, these networks extend up to 30 cm downward into the sediment and represent a behaviour adapted to a specific ecological niche found only on intertidal fine-sand or mud flats (Bromley 1990). Thus they are not likely analogues for the Gander Lake burrows. Likewise, although some deep-marine planispiral traces may have been used for cultivation of bacteria or fungi (Seilacher

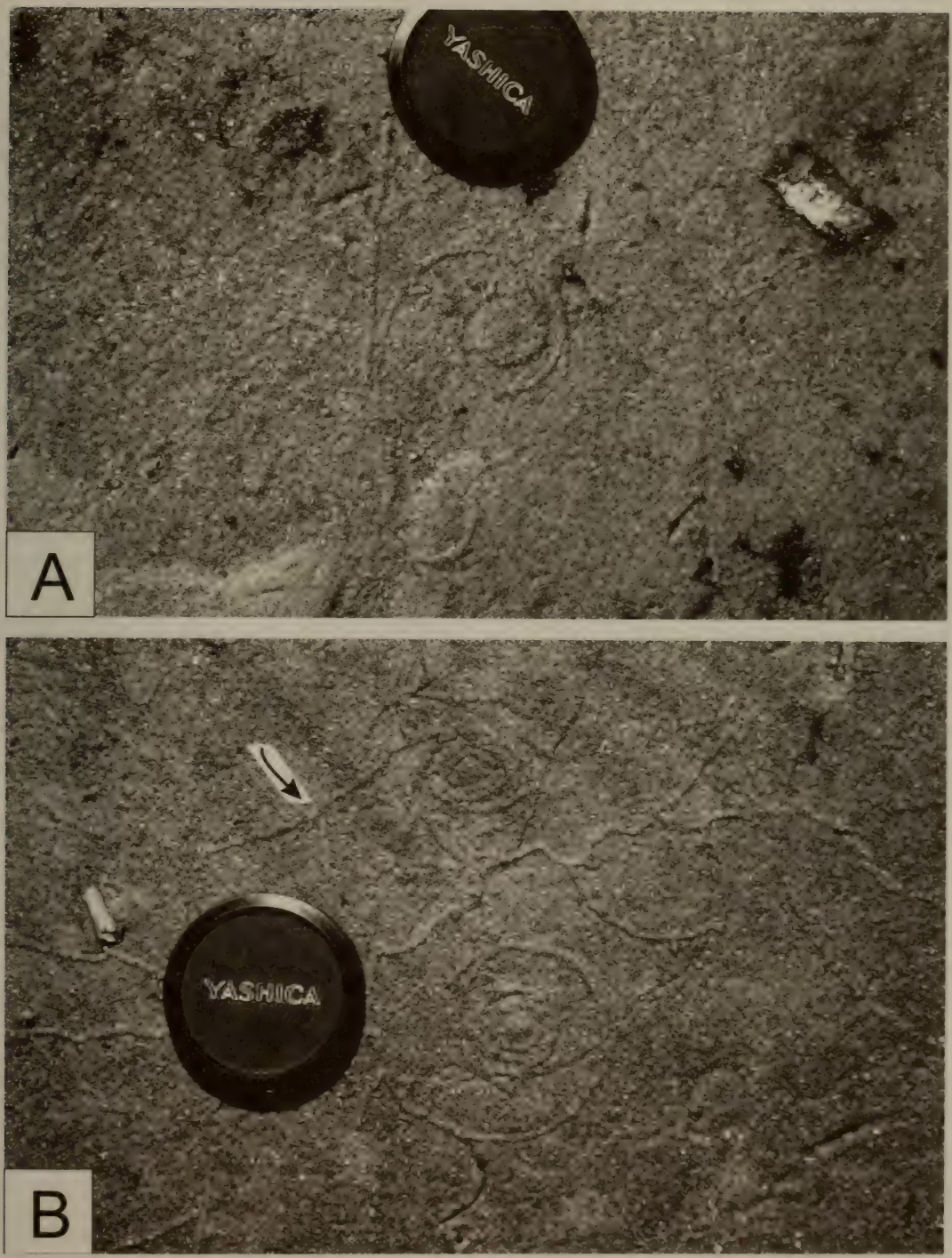


Figure 2: Photographs of the planispiral burrows. Lens cap is 56 mm in diameter. (A) Burrow with slightly raised central area and progressively more open outward coiling. Note possible continuation of burrow toward bottom of photograph. (B) Planispiral burrow near top of photograph shows tight, slightly irregular coiling and continues to left of picture as a simple, horizontal burrow (indicated by arrow). Example near bottom of photograph displays coils that become less tight outward and a raised central area. Note horizontal burrow with apparent branches extending from centre of photograph to top right.

1977; Miller 1991), such structures were presumably open burrows while the present material is apparently backfilled.

In modern deep-marine settings, planispiral coils are commonly produced by detritus-feeding enteropneusts (acorn worms: Hemichordata) as faecal castings (Bourne and Heezen 1965; Heezen and Hollister 1971). Planispiral burrowing permits efficient mining of nutrients without reburrowing previously processed sediment (Bourne and Heezen 1965). Although the present material consists of infaunal burrows rather than faecal castings, deposit feeding would have been an effective strategy and is most probably the behaviour represented by the burrows. Previously reported shallow-marine (Ecca Group, Permian, South Africa; Mason et al. 1983) and non-marine (Mansfield Formation, Lower Pennsylvanian, Indiana; Archer and Maples 1984) planispiral trace fossils probably also represent deposit feeding.

Any comment regarding a possible producer must be speculative. However, the irregularly annulate nature of the Gander Lake burrows is similar to the appearance of feeding burrows produced by some small, non-marine arthropods, notably beetles (cf., Chamberlain 1975; Ratcliffe and Fagerstrom 1980). Metz (1987, p. 190) documented a ground beetle larva that produced a planispiral trace in an ephemeral puddle, although the trace's detailed morphology was quite different from the present examples.

Palaeoecological Significance

These burrows may help to address the origin of structures from the Upper Triassic of Pennsylvania, described by Metz (1999) as probable scratch circles produced by plants. Metz (1999) figured a set of roughly concentric, arc-shaped structures in convex relief on the bottom surface of a bed. He discussed their possible origin as feeding burrows, but rejected this interpretation based on the paucity of infaunal burrows in the rest of the succession. However, the structures described by Metz (1999) show lobate terminations and cross-sections, rather than the sharper, more angular morphology typical of other documented scratch circles (Metz 1991). They also lack the strong concentricity that typifies Recent (e.g., Brookfield 1992) and ancient (Prentice 1962; Metz 1991; Rindsberg 1994) scratch circles. The material described by Metz (1999) somewhat resembles the more irregular examples of the burrows described herein and may thus represent incompletely preserved planispiral burrows. Interestingly, like the Gander Lake material, the material described by Metz (1999) comes from a lake-margin setting, although the Triassic material apparently formed on a silty to muddy substrate rather than a sandy one.

In the stratigraphic record, planispiral traces are most commonly reported from deep-marine deposits, where they are part of an important morphologic category of trace fossils, the graphoglyptids (Miller 1991). In rare cases, however, such traces have been reported from shallow-marine (Mason et al. 1983) and non-marine (floodplain) deposits (Archer and Maples 1984). In the Recent, planispiral traces have been reported from the deep sea (Bourne and Heezen 1965) and, in one case, from ephemeral puddles (Metz, 1987). The intertidal burrow networks of *Paraonis fulgens* (see above), represent a more complex and "three-dimensional" style of burrowing (Schäfer 1972; Risk and Tunnicliffe 1978) and so are not strictly comparable to the burrows described in this contribution.

To my knowledge, this is the first formal report of planispiral burrows from any lacustrine setting. It thus adds to a growing database of studies illustrating the potentially high diversity of non-marine traces, both Recent and fossil (e.g., Tevesz and McCall 1982; Metz 1987; Maples and Archer 1989; Pickerill 1992; Buatois et al. 1998). In addition, this report, along with those of Metz (1987) and Archer and Maples (1984), indicates that the presence of planispiral burrows in a stratigraphic succession cannot, in and of itself, be used as evidence for a marine or marine-influenced depositional setting. Finally, this material re-emphasises the potentially broad environmental distributions of many common trace fossil taxa. (For additional examples, see, e.g., Fitzgerald and Barrett 1986; Pickerill 1990, 1995; Stanley and Pickerill 1993).

Acknowledgments

The burrows described in this paper were found during a study of the tectonic history of central Newfoundland, conducted by Laurel Goodwin and funded by a Natural Sciences and Engineering Research Council operating grant to Paul F. Williams (University of New Brunswick). I thank Laurel and Paul for encouraging ancillary research. J.-P. Zonneveld, R. Metz, G. C. Cadée, and two anonymous, journal-appointed reviewers are thanked for their reviews of this manuscript. B. Rutley provided sterling assistance with photographs. Geological Survey of Canada contribution 2000190.

Literature Cited

Archer, **A. W.**, and **C. G. Maples**. 1984. Trace-fossil distribution across a marine-to-nonmarine gradient in the Pennsylvanian of southwestern Indiana. Journal of Paleontology 58: 448- 466.

Batterson, **M. J.**, and **S. Vatcher**. 1991. Quaternary geology of the Gander (NTS 2D/15) map area. *In* Current Research, Newfoundland Department of Mines and Energy, Geological Survey Branch, Report 91-1, pages 1-12.

Bourne, **D. W.**, and **B. C. Heezen**. 1965. A wandering enteropneust from the abyssal Pacific and the distribution of "spiral" tracks on the sea floor. Science 150: 60-63.

Brookfield, **M. E.** 1992. Eolian systems. Pages 143-156 *in* Facies Models: Response to Sea Level Change. *Edited by* R. G. Walker and N. P. James. Geological Association of Canada, St. John's, Newfoundland.

Buatois, **L. A.**, and **M. G. Mángano**. 1993. The ichnotaxonomic status of *Plangtichnus* and *Treptichnus*. Ichnos 2: 217-224.

Buatois, L. A., M. G. Mángano, J. F. Genise, and **T. N. Taylor**. 1998. The ichnologic record of the continental invertebrate invasion: evolutionary trends in environmental expansion, ecospace utilization, and behavioral complexity. Palaios 13: 217-240.

Bromley, R. G. 1990. Trace Fossils: Biology and Taphonomy. Unwin Hyman, London. 280 pages.

Chamberlain, C. K. 1975. Recent lebensspuren in nonmarine aquatic environments. Pages 431-458 *in* The Study of Trace Fossils. *Edited by* R. W. Frey. Springer-Verlag, New York.

Fitzgerald, P. G., and **P. J. Barrett**. 1986. *Skolithos* in a Permian braided river deposit, southern Victoria Land, Antarctica. Palaeogeography, Palaeoclimatology, Palaeoecology 52: 237- 247.

Frey, R. W., S. G. Pemberton, and **T. D. A. Saunders**. 1990. Ichnofacies and bathymetry: a passive relationship. Journal of Paleontology 64: 155-158.

Hantzschel, W. 1975. Treatise on Invertebrate Paleontology, Part W. Miscellanea, Supplement 1. Trace Fossils and Problematica. Geological Society of America, Boulder. 269 pages.

Heezen, B. C., and **C. D. Hollister**. 1971. The Face of the Deep. Oxford University Press, New York. 659 pages.

Huckriede, R. 1952. Eine spiralförmige Lebensspur aus dem Kulmkieselschiefer von Biedenkopf an der Lahn (*Spirodesmos archimedeus* n. sp.). Paläontologische Zeitschrift 26: 175-180.

Jenness, S. E. 1960. Late Pleistocene glaciation of eastern Newfoundland. Bulletin of the Geological Society of America 71: 161-179.

Maples, C. G., and **A. W. Archer**. 1989. The potential of Paleozoic non-marine trace fossils for paleoecological interpretations. Palaeogeography, Palaeoclimatology, Palaeoecology 73: 185-195.

Mason, T. R., I. G. Stanistreet, and **R. Tavener-Smith**. 1983. Spiral trace fossils from the Permian Ecca Group of Zululand. Lethaia 16: 241-247.

Metz, R. 1987. Insect traces from nonmarine ephemeral puddles. Boreas 16: 189-195.

Metz, R. 1991. Scratch circles from the Towaco Formation (Lower Jurassic), Riker Hill, Roseland, New Jersey. Ichnos 1: 233-235.

Metz, R. 1999. Scratch circles: a new specimen from a lake-margin deposit of the Passaic Formation (Upper Triassic), Douglassville, Pennsylvania. Northeastern Geology and Environmental Sciences 21: 179-180.

Miller, W., III. 1991. Paleoecology of graphoglyptids. Ichnos 1: 305-312.

Pickerill, R. K. 1990. Nonmarine *Paleodictyon* from the Carboniferous Albert Formation of southern New Brunswick. Atlantic Geology 26: 157-163.

Pickerill, R. K. 1992. Carboniferous nonmarine invertebrate ichnocoenoses from southern New Brunswick, eastern Canada. Ichnos 2: 21-35.

Pickerill, R. K. 1995. Deep-water marine *Rusophycus* and *Cruziana* from the Ordovician Lotbinière Formation of Quebec. Atlantic Geology 31: 103-108.

Prentice, J. E. 1962. Some sedimentary structures from a Weald Clay Sandstone at Warnham Brickworks, Horsham, Sussex. Proceedings of the Geologists' Association 73: 171-185.

Ratcliffe, B. C., and **J. A. Fagerstrom**. 1980. Invertebrate lebensspuren of Holocene floodplains: their morphology, origin and paleoecological significance. Journal of Paleontology 54: 614-630.

Rindsberg, A. K. 1994. Ichnology of the Upper Mississippian Hartselle Sandstone of Alabama, with notes on other Carboniferous formations. Geological Survey of Alabama, Bulletin 158. 107 pages.

Risk, M. J., and **V. J. Tunnicliffe**. 1978. Intertidal spiral burrows: *Paraonis fulgens* and *Spiophanes wigleyi* in the Minas Basin, Bay of Fundy. Journal of Sedimentary Petrology 48: 1287-1292.

Röder, H. 1971. Gangsysteme von *Paraonis fulgens* Levinsen 1883 (Polychaeta) in okologischer, ethologischer und aktuopaläontologischer Sicht. Senckenbergiana Maritima 3: 3-51.

Schäfer, W. 1972. Ecology and Paleoecology of Marine Environments. University of Chicago Press, Chicago. 568 pages.

Seilacher, A. 1977. Pattern analysis of *Paleodictyon* and related trace fossils. Pages 289-334 *in* Trace Fossils 2. *Edited by* T. P. Crimes and J. C. Harper. Geological Journal, Special Issue 9.

Stanley, D. C. A., and **R. K. Pickerill**. 1993. Shallow marine *Paleodictyon* from the Upper Ordovician Georgian Bay Formation of southern Ontario. Atlantic Geology 29: 115-119.

Tevesz, M. J. S., and **P. L. McCall**. 1982. Geological significance of aquatic non-marine trace fossils. Pages 257-285 *in* Animal-Sediment Relations. *Edited by* P. L. McCall and M. J. S. Tevesz. Plenum Publishing Company, New York.

Received 7 February 2002
Accepted 20 April 2004

Have Lesser Scaup, *Aythya affinis*, Reproductive Rates Declined in Parkland Manitoba?

David N. Koons[1] and Jay J. Rotella

Department of Ecology, Montana State University, Bozeman, Montana 59717
[1]Present address: School of Forestry and Wildlife Sciences, 108 M. White Smith Hall, Auburn University, Alabama 36849 USA

Koons, David N., and Jay J. Rotella. 2003. Have Lesser Scaup, *Aythya affinis*, reproductive rates declined in parkland Manitoba? Canadian Field Naturalist 117(4): 582-588.

Long-term surveys indicate that the scaup populations have declined over the past 20 years, and that this is probably the result of decreases in Lesser Scaup (*Aythya affinis*) rather than Greater Scaup (*Aythya marila*) numbers. To identify factors possibly related to the decline, we estimated demographic parameters for a local population of Lesser Scaup at Erickson, Manitoba, that was well studied before declines occurred and compared these estimates to historic rates. On average, nests were initiated later than in the past, and recent estimates of nesting success and duckling survival were lower than historical estimates. Breeding-season survival of adult females was estimated as 72.6%, with most (83%) mortality occurring during nesting. Current estimates of demographic rates at Erickson are too low to maintain a stable local population, and suppressed reproductive rates might be the proximate cause of the local population decline.

Key Words: Lesser Scaup, *Aythya affinis*, demographic parameters, duckling survival, female survival, life history, nesting success, Manitoba.

North American scaup numbers have been declining for over 20 years (Afton and Anderson 2001), and, in recent years, numbers have approached record lows (Garrettson et al. 2003). The decline in scaup numbers is more likely related to decreases in Lesser Scaup (*Aythya affinis*) rather than Greater Scaup (*Aythya marila*) [Afton and Anderson 2001]. While the majority of declines have taken place in the boreal forest where 68% of scaup breed, numbers at historically important breeding locales in the prairie-parklands have declined as well (Austin et al. 1998; Afton and Anderson 2001; Koons and Rotella 2003).

Hypotheses proposed to explain Lesser Scaup population decline (Austin et al. 2000; Afton and Anderson 2001) convey how possible changes in the environment have led to corresponding changes in demographic parameters (i.e., survival and reproductive rates) and thus, population size. However, despite our knowledge of some aspects of the life history of Lesser Scaup (Austin et al. 1998), information is lacking on potential changes in demographic parameters over the past 20 years, and environmental factors affecting demographic parameters. Specifically, few estimates of survival and reproductive parameters have ever been published for Lesser Scaup (see Austin et al. 1998), and there are only five published estimates from data collected during the past 20 years (Dawson and Clark 1996, 2000; Fournier and Hines 2001; Koons and Rotella 2003; Rotella et al. 2003).

A complete set of demographic parameters was estimated for Lesser Scaup on only one study area near Erickson, Manitoba (Afton 1984; Rotella et al. 2003) prior to the decline of the continental population. Estimates of demographic rates for Erickson scaup came primarily from Afton (1984) along with a few additional estimates (Rogers 1964; Hammell 1973; Rotella et al. 2003). Furthermore, using simple linear regression Koons (unpublished data) found that numbers of scaup detected on survey strata (Stratum 40; transect 6, segments 3 and 4; transect 4, segment 4 [raw data collected by the U.S. Fish and Wildlife Service, Laurel, Maryland, USA]) near Erickson were stable from 1970 to 1981 ($\beta = 7.2$; SE = 11.5; $p = 0.55$) but declined from 1982 to 2002 ($\beta = -16.5$; SE = 6.7; $p = 0.02$). We took advantage of information on Lesser Scaup at Erickson and conducted a study with the objectives of (1) estimating demographic parameters and comparing them with those estimated prior to the local population decline, and (2) evaluating relationships between demographic parameters and attributes of individual birds and environmental covariates.

Study Area

We conducted work on a 28.5-km^2 site (including the site used by Rogers [1964], Hammell [1973], Afton [1984], and Austin and Frederickson [1986]) located 4.8 km south of Erickson, Manitoba (50° 30'N, 99° 55'W) on the Riding Mountain Plateau in the parkland region. Land cover consisted of numerous small wetlands (12-19 wetlands/km^2), and patches of aspen (*Populus tremuloides* and *Populus balsamifera* [comprising 12% of the landscape]), within a landscape dominated by cereal grain agriculture (42%), grassland and pasture (17%), and hayland (15% [data acquired from analysis of 1994 black-and-white aerial photographs]).

Field Methods

Trapping and Telemetry

We trapped, radiomarked, and followed females during 15 May – 1 September in 1999 and 2000. We used decoy traps to capture some females each spring before they initiated nests. Each decoy trap contained a live captive-reared female scaup (Anderson et al. 1980) or a plastic decoy and mirrors. Nests of unmarked females were located using systematic foot searches, a chain drag (Klett et al. 1986), a rope drag, observations of females in or near nesting cover, or combinations of these methods. At nests that survived past five days of incubation, we trapped females using Weller nest traps (Weller 1957). For each female trapped, we recorded body mass (± 5 g), and estimated age using eye color (Trauger 1974). We outfitted each female with a 9-g prong-and-suture radio transmitter containing a 12-hr motion-mortality switch (Advanced Telemetry Systems, Isanti, Minnesota, USA) and a U.S. Fish and Wildlife Service aluminum leg band. Each female also was outfitted with a unique combination (color and shape) of nylon nasal disks (Lokemoen and Sharp 1985). Nest-trapped birds were anesthetized with propofol after handling to reduce nest abandonment (Machin and Caulkett 1998). Birds were released at the place of capture within 20 min of being removed from a trap. We then monitored radiomarked females throughout the breeding season with hand-held antennas, and truck-mounted or airplane-mounted null-peak antenna systems. Several times each week, we estimated each female's location and monitored survival status.

Nesting Success

Nests of non-radiomarked females were visited every 4 to 6 days to determine fate (Bart and Robson 1982). For nests of radiomarked females, we used female locations to monitor nest status. If a radiomarked female was not located at her nest for ≥ 24 hr, we checked the nest to determine its status. We defined a successful nest as one that hatched at least one egg (Klett et al. 1986). We recorded total clutch size at each nest that survived to incubation. Because full clutch size could not be accurately determined for three nests that were parasitized by Redheads (*Aythya americana*, [Sayler 1985]) or two nests found after a flooding event, we excluded these nests from clutch-size analyses. We also excluded the one known re-nest of a radiomarked female from the clutch-size analysis because Afton (1984) excluded re-nests.

Duckling Survival

To estimate duckling survival, we followed marked females that hatched nests, and we attempted to count the number of ducklings in each brood every 2 days until all ducklings in the brood died or reached 28 days of age. We used 28 days as an endpoint because duckling mortality is uncommon in ducklings > 4 weeks of age (Afton 1984; Dawson and Clark 1996). Whenever we suspected that a female had lost her brood, we repeatedly watched the wetland(s) being used by that female and radiotracked her intensively for a week. We concluded that a female had lost her brood if she was never seen with ducklings during that week. If a brood was not readily visible during a brood count, we made noise from a distance, which usually caused the brood to swim to the middle of the pond. Only two ponds on the study area had > 1 scaup brood on them, and duckling age was notably different among these broods. Still, to alleviate possible bias associated with brood mixing, we verified that the size and feather development of each duckling in a brood was consistent with the known age of that female's brood (Gollop and Marshall 1954).

Data Analyses

Nesting Success

To estimate scaup nesting success and to evaluate factors related to nesting success, we used data on nest fates (survived or died) for intervals of varying lengths (4- to 6-day intervals for non-radiomarked females, 1-day interval for radiomarked females). Because Afton's (1984) historic estimate of nesting success on our study area did not include data from island nests, we excluded three island nests. We evaluated factors potentially related to nesting success using generalized linear models (McCullogh and Nelder 1989) that employed a binomial distribution of errors for fate and a log-link function, and estimated potential observer-effects (Rotella et al. 2000) as well as regression coefficients for covariates of interest. This is a simple extension of the commonly used maximum likelihood estimator of Mayfield's daily survival rate (DSR) (Mayfield 1975; Johnson 1979; Bart and Robson 1982), which makes the same assumptions but allows one to examine the effect of visiting the nest on DSR.

We developed a simple a priori list of candidate models and considered each of the following covariates to be potentially related to DSR of nests: habitat type (upland or over-water nesting site), observer-effect (the effect of investigators visiting the nest), year, and period of nesting season. Because of the sparse data set, we could not consider calendar date as a continuous covariate, but had to group the survival intervals into three periods of the nesting season (early [12 June to 2 July], middle [3 July to 24 July], and late [25 July to 15 August]). According to guidelines provided by Burnham and Anderson (1998), the complexity of our model list was constrained by the amount of data available. Thus, we only considered univariate effects in our models. Support for each model was evaluated with Akaike's Information Criterion adjusted for sample size (AIC_c) and Akaike weights (Akaike 1973; Burnham and Anderson 1998:

51, 124). We considered the best approximating model to be that with the lowest AIC_c value and highest Akaike weight.

Because modeling was done on a log-transformed response variable, we estimated DSR and its confidence limits by back-transforming the regression equation and using an interval length of 1 day (Rotella et al. 2000). Each slope parameter (β_i) that appeared in the best approximating models was assessed based on the extent to which 95% confidence intervals for $\hat{\beta}_i$s overlapped zero (Graybill and Iyer 1994).

Duckling Survival

We defined duckling survival as the proportion of all ducklings that survived from hatch to 28 days of age and brood survival as the proportion of broods that had at least one duckling survive for 28 days. Because some females abandoned their broods before 28 days of age, we used right-censored data (White and Burnham 1999); thus, brood survival estimates were not integer values. We assumed that brood amalgamation did not occur because we never saw a brood size increase and the age of each duckling was consistent with the age of the brood. To estimate duckling survival, we used a generalized linear model with binomial distribution of errors for fate and a logit-link function (McCullogh and Nelder 1989) and estimated the standard error by treating broods as clusters in a cluster sampling design (Flint et al. 1995). Because the sample of broods was too small to warrant comparison of competing models (see Results), we pooled yearly data and did not evaluate relationships between duckling survival and ecological covariates.

Female Survival

We used telemetry data (sequences of 1- to 6-day intervals collected throughout each field season), generalized linear models (McCullogh and Nelder 1989), and model-selection methods described above to estimate DSR for adult female scaup. Models estimated DSR for three periods: (1) non-maternal (DSR_{nm}, days spent on the study area when a female was not nesting or rearing a brood), (2) nesting (DSR_n), and (3) brood rearing (DSR_{br}). Period-specific estimates of DSR were then used to estimate the average breeding-season survival ($\hat{BS}$) of the local population with the following equation:

$$\hat{BS} = \hat{NB} \cdot (\hat{DSR}_{nm}^{\hat{d}_{nm}}) + \hat{FN} \cdot (\hat{DSR}_{nm}^{\hat{d}_{nm}}) \cdot (\hat{DSR}_n^{\hat{d}_n}) + \hat{SN} \cdot (\hat{DSR}_{nm}^{\hat{d}_{nm}}) \cdot (\hat{DSR}_n^{\hat{d}_n}) \cdot (\hat{DSR}_{br}^{\hat{d}_{br}}),$$

where $\hat{NB}$ is the estimated proportion of females that were non-breeders; $\hat{FN}$ is the estimated proportion of females that attempted to nest but failed on all attempts; $\hat{SN}$ is the estimated proportion of females that attempted to nest and succeeded; and $\hat{d}_{nm}$, $\hat{d}_n$, $\hat{d}_{br}$, and are the mean number of days spent in each of the three periods, respectively. We used Afton's (1984) four-year average of 0.157 to estimate $\hat{NB}$ because our data were inadequate for estimating this parameter. Our telemetry data were used to estimate the remaining parameters.

Results

We captured and radio-marked 34 females (n = 18 in 1999, n = 16 in 2000). Of these females, six were trapped during the pre-nesting period and five of these were known to nest (one left the study area before nesting could be confirmed). Of these six females, three were one year old, two were two years old, and one was ≥ four years old. Of all females caught (not including re-sights of marked females), 10 were one year old, 16 were two years old, one was three years old, and seven were ≥ four years old. This sample provided data for 34 nests (including one known re-nest), nine broods, and female survival. We found 22 additional nests, and thus, located a total of 56 scaup nests, 49 of which provided data for estimating nesting success (seven nests were abandoned after the first nest visit). Fifty-seven percent of Lesser Scaup nests were located over water up to 1 m deep. Average nest-initiation dates for 1999 (n = 33) and 2000 (n =21) were 24 June (SE = 2 d, median = 25 June, range = 31 May – 10 July) and 25 June (SE = 2 d, median = 26 June, range = 11 June – 20 July), respectively. Estimates of mean clutch size were 9.9 (n = 26, SE = 0.33, 95% CI = 9.3 to 10.6, range = 4 – 12) and 9.4 (n = 13, SE = 0.31, 95% CI = 8.8 to 10.0, range = 7 – 11) in 1999 and 2000, respectively.

Nesting Success

Our visits to 49 scaup nests created 288 intervals that ranged from 1 to 6 days in length. Estimated DSR was 0.940 (95% CI = 0.913 to 0.967) in 1999 and 0.943 (95% CI = 0.910 to 0.976) in 2000. Corresponding maximum-likelihood estimates of nesting success were 10.8% and 12.1%, respectively.

The best approximating model of DSR contained no observer, environmental, or year effects. This null model estimated DSR as 0.941 (95% CI = 0.921 to 0.962, 11.2% nesting success). The "period of nesting season" and "habitat type" models had ΔAIC_c values < 2.0, but these parameters were imprecise and had 95% confidence intervals that included zero.

Duckling Survival

Over two years, eight different radiomarked females hatched a total of nine broods and 54 ducklings (one female studied in both years; four broods in 1999 and five in 2000). The estimated 28-day duckling survival rate was 0.20 (95% CI = 0.00 to 0.58), and estimated brood survival rate was 0.48 (95% CI = 0.19 to 0.79).

Female Survival

We recorded no deaths during the non-maternal period (n = 25 females, 943 observation days). Given that our estimated DSR for the non-maternal period was 1.0, we checked if confidence intervals for estimated DSR in other periods included 1.00 and whether DSRs differed between the nesting (five mortalities) and brood-rearing (one mortality) periods. A model that estimated a common survival rate for nesting and brood-rearing (n = 29 females, 411 observation days;

estimated DSR = 0.986, 95% CI = 0.975 to 0.997) periods was better ($\Delta AIC_c = 0.00$) than a model that generated period-specific estimates ($\Delta AIC_c = 1.34$). We estimated that 74.9% of radiomarked females attempted to nest but failed in all attempts, and 9.4% hatched young. The average number of days that a female was observed was 82, and average numbers of days spent in the nesting and brood-rearing periods were 26 and 19, respectively. We then incorporated these estimates into the breeding-season survival equation:

$$\hat{BS} = 0.157 \cdot (1.00^{82}) + 0.749 \cdot (1.00^{56}) \cdot (0.986^{26}) + 0.094 \cdot (1.00^{37}) \cdot (0.986^{26}) \cdot (0.986^{19})$$

The weighted product estimate of breeding-season survival produced by the model that pooled nesting and brood-rearing periods was 0.726 (95% CI = 0.575 to 0.932). By excluding the non-breeding component of the population, we estimated that the breeding-season survival for the component that attempted to breed at least once was 0.675 (95% CI = 0.496 to 0.919).

Discussion

Nesting

Our data suggest that nesting success of Lesser Scaup was poor at Erickson in recent years and similar to that from a concurrent study in parkland Saskatchewan (0.03, 95% CI = 0.004 to 0.12 [Brook 2002]). Nesting success at both locations may be lower than average values for the parklands (0.295), prairies (0.373), and boreal forest (0.572) [see Austin et al. 1998]. Although our estimate of nesting success was imprecise, the point estimate was much lower than the mean estimate from 1977-1980 at Erickson (Table 1). Further study will be needed on larger samples of nests and potential covariates of nest survival to understand why nesting success is so low at Erickson, and why recent estimates from the western boreal forest of Canada (Fournier and Hines 2001; Brook 2002) were lower than historic estimates (Townsend 1966; citations in Austin et al. 1998). Additionally, future studies need to examine the prevalence of suppressed nesting success across the breeding range of Lesser Scaup (Afton and Anderson 2001). Given that nesting success is thought to play a major role in the population dynamics of duck species, a decline in nesting success could have large impacts on population dynamics (Johnson et al. 1992); however, reasons for suppressed nesting success are not known.

Evidence from broad-scale studies of a variety of duck species suggests that nesting success of parkland and prairie-nesting ducks declined between 1935 and 1990 (Beauchamp et al. 1996), while the amount of cultivated land, predator diversity, and predator abundance all increased (Sargeant et al. 1993). However, the amount of cultivated land near Erickson during our study was similar to that of the early 1970s (Hammell 1973), and we had limited ability to make inferences about factors related to nesting success. Interestingly, Lesser Scaup bred sympatrically with one of their closest phylogenetic relatives, the Ring-necked Duck (*Aythya collaris*) [Livezey 1996], at Erickson and both nested at similar times of the year in similar habitats (Koons and Rotella 2003). However, they did not appear to compete for breeding territories. Nevertheless, Ring-necked Duck nesting success at Erickson was 2.9 times higher than that of Lesser Scaup. Further, the local Ring-necked Duck population is increasing while the Lesser Scaup population is decreasing (Koons and Rotella 2003). Thus, local habitat conditions might be suitable for scaup nesting. We speculate that changes in either food quantity or quality away from the breeding grounds have negatively impacted scaup physiology and nutrient reserves (Afton and Anderson 2001, Anteau 2002), which could in turn affect reproductive behavior and success.

Then again, we did not find a difference in fecundity between time periods at Erickson. Our estimate of mean clutch size (9.7) was similar to the pre-1981 estimate of 9.8 (Hammell 1973, Afton 1984). However, our mean date of nest initiation was delayed by one week when compared to 1977-1980 (Table 1). If females are returning to the breeding grounds in poorer physical condition than in the past, as Afton and Anderson (2001) have hypothesized, then one consequence could be delayed breeding, which we observed. Dawson and Clark (2000) found a negative relationship between hatch date and recruitment probabilities of Lesser Scaup ducklings. Thus, delayed breeding has the potential to negatively affect scaup populations. Future studies should determine the occurrence, causes, and consequences of late nesting.

Duckling Survival

Our point-estimate of duckling survival (0.20) was less than one third of the estimated mean for 1977-1980 (Table 1). Such a change would have large negative impacts on population size. Our estimate of duckling survival rate is among the lowest ever reported for ducks nesting at northern latitudes (see Rotella and Ratti 1992; Grand and Flint 1996) and is lower than estimates for Lesser Scaup in the western boreal forest of Canada (0.61, Brook 2002) and parklands of Saskatchewan (0.38, Dawson and Clark 1996). Low duckling survival could be related to delayed nest initiation. In other duck species nesting in the mid-continent, later hatched ducklings have poorer survival (Rotella and Ratti 1992; Dzus and Clark 1998; Guyn and Clark 1999). One study suggests that this trend may not hold for scaup (see Dawson and Clark 1996), but these same authors found that recruitment declines with hatch date (Dawson and Clark 2000). The ultimate effect of hatch date on recruitment would negate its effect on duckling survival.

Alternatively, low duckling survival may be associated with possible changes in the predator community, food abundance, or the prolonged wet conditions

TABLE 1. Period-specific estimates of Lesser Scaup demographic parameters at Erickson, Manitoba.

	1970-1971[a]			1977-1980[b]			1999-2000[c]		
Parameter	*n*	$\bar{x}$	95% C.I.	*n*	$\bar{x}$	95% C.I.	*n*	$\bar{x}$	95% C.I.
Nest-initiation date				78	15 June	10 – 20 June	54	24 June	21 – 27 June
Clutch size	35	9.0	8.6 – 9.4	77	10.3	10.1 – 10.5	39	9.7	9.2 – 10.2
Nesting success				129	0.31[d]	0.23 – 0.39	49	0.11	0.05 – 0.25
Duckling survival				39	0.68	0.43 – 0.92	9	0.20	0.00 – 0.58

[a] – The weighted mean across years from Hammell's (1973) study.
[b] – The weighted means across years from Afton's (1984) study.
[c] – The weighted means across years from this study
[d] – Afton (1984) found most of his nests in the early laying stages (1-3 d of age) by observing females fly or swim to the nest (A. Afton, personal communication). Thus, his estimates of apparent nesting success should be comparable to ours based on estimation of daily survival rate but may be biased high to a minor extent. *Note*: Rogers (1964) and Hammell (1973) estimated nesting success, but their methods and estimators are not comparable to ours.

in the study area prior to and during our study. Specifically, prolonged wetness may have led to increased abundance of Mink, *Mustela vison,* which are known to prey upon ducklings (Arnold and Fritzell 1987).

Female Survival

This is the first study to provide a known-fate estimate of breeding-season survival of adult female scaup. Our estimate of local breeding-season survival (0.726) is the lowest reported estimate for any northern-latitude breeding duck (Ringleman and Longcore 1983; Cowardin et al. 1985; Kirby and Cowardin 1986; Dwyer and Baldassarre 1993; Petrie et al. 2000). If we exclude non-breeders, our estimate is even lower (0.675, see Results). Historic estimates of breeding-season survival do not exist at Erickson. However, from 1977 to 1981 the annual survival of adults and juveniles was 0.59 (SE = 0.06 [Rotella et al. 2003]). If breeding-season survival equaled our estimate during 1977 to 1981, then survival during the non-breeding season would have averaged 0.81. This estimate seems high considering the birds must survive about nine months, two migrations, hunting season, and harsh weather during the non-breeding season (Blums et al. 2002). Nevertheless, our estimate of breeding-season survival is statistically similar to that for scaup at St. Denis, Saskatchewan, during 1992 to 2001 (0.82, SE = 0.12 [Rotella et al. 2003]), and to that at Yellowknife, Northwest Territories, during 1999 and 2000 (42 d estimate = 0.80, SE = 0.09 [Brook 2002]). All estimates of female scaup mortality on the breeding grounds are high, which could have substantial effects on population growth rate (Koons 2001), and could be contributing to the declines of Lesser Scaup populations.

Our data indicate that survival was lower during maternal periods (nesting and brood-rearing) than during non-maternal periods, indicating that it is costly for a mother to attend to young. Further, almost all of the mortality (83%) occurred at nests. Because we found three dead female scaup in Mink dens and noted canine marks that matched those of Mink on all other dead females, we believe that Mink killed all six females. Similarly, Afton (1984) noted that seven marked females were killed on nests in 1979 and 1980 (Mink killed four and Red Fox [*Vulpes vulpes*] killed three). Future studies should examine the predator-prey interactions between Mink and scaup.

Study Limitations

Because of local population decline (see Introduction), the population of scaup that existed during our study was small and prevented us from achieving desired sample sizes. This limited our ability to detect environmental factors that might influence demographic rates. We acknowledge that our results for parameters estimated from radiomarked females would be biased low if transmitters negatively affected females or if a trapping bias existed. Across all demographic rates, we did not detect marker-effects nor did we detect a trapping bias across female age, body size, or mass (unpublished analyses). However, we must note that our sample sizes were too small to adequately test for such effects. Furthermore, we did not explicitly design our study to collect comparable data for birds with and without radios. Still, lightweight radio-transmitters, similar to ours, have been used on Lesser (Custer et al. 1996; Brook and Clark 2002) and Greater Scaup (P. L. Flint and J. B. Grand personal communication) without obvious effects. Furthermore, five out of six birds that were marked before the nesting season did nest (the other bird left the study area).

Conclusions

Our results indicate that the Erickson scaup population may be nesting later than in the past and presently has lower nesting success and duckling survival than in the past. Furthermore, adult female breeding-season survival was alarmingly low during our study. In general, these findings are consistent with the hypothesis that reproductive success has declined (Austin et al. 2000; Afton and Anderson 2001). Our estimates were not precise enough to allow us to conclude definitively that reproductive success has declined. Nevertheless, these demographic parameters may have been

at low levels during our study due to alteration of habitat on and off the breeding grounds, prolonged wet conditions on the study area and associated numerical responses by key predators, or all. Apart from three-year olds, the age structure of our captured population was approximately similar to that during Afton's study (1984). While age structure has strong potential to affect scaup demography (Afton 1984) and short-term population dynamics (Fox and Gurevitch 2000), we do not believe age structure was responsible for the low reproductive success of scaup in 1999 and 2000 at Erickson.

Assuming nesting success and breeding-season survival were low, and that most female mortality occurs at nests, it is likely that management aimed toward increasing the security of nests will benefit both nesting success and survival of females. Before such management action can be taken across large areas, demographic parameters of scaup populations need to be estimated across broader spatial and temporal scales to examine the ubiquity of our results. Data are especially needed for the boreal forest. Additionally, large samples of marked birds will be required to effectively examine ecological factors related to, and responsible for, variation in demographic parameters. Lastly, we suggest that future research address physiological and cross-seasonal factors related to Lesser Scaup breeding chronology and success to test other hypotheses and ultimate factors related to the decline in scaup numbers (Afton and Anderson 2001).

Acknowledgments

We thank J. E. Austin, A. J. Erskine, M. S. Lindbergh, and two anonymous referees for their comments on an earlier version of this manuscript. We also thank A. D. Afton for his pioneering research on the demography of the Erickson scaup population, and our many hard-working assistants for their long hours in the field. The Delta Waterfowl and Wetlands Research Station, the Institute for Wetlands and Waterfowl Research of Ducks Unlimited Canada, the Minnesota Waterfowl Association, and Montana State University provided financial support for this research.

Literature Cited

Afton, A. D. 1984. Influence of age and time on reproductive performance of female Lesser Scaup. Auk 101: 255-265.

Afton, A. D., and **M. G. Anderson.** 2001. Declining scaup populations: a retrospective analysis of long-term population and harvest survey data. Journal of Wildlife Management 65: 781-796.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* International symposium on information theory. Second edition. *Edited by* B. N. Petran and F. Csaki. Akademiai Kiado, Budapest, Hungary.

Anderson, M. G, R. D. Sayler, and **A. D. Afton.** 1980. A decoy trap for diving ducks. Journal of Wildlife Management 44: 217-219.

Anteau, M. J. 2002. Nutrient reserves of Lesser Scaup during spring migration in the Mississippi flyway: A test of the spring condition hypothesis. M.S. thesis, Louisiana State University, Baton Rouge, Louisiana.

Arnold, T. W., and **E. K. Fritzell.** 1987. Food habits of prairie Mink during the waterfowl breeding season. Canadian Journal of Zoology 65: 2322-2324.

Austin, J. E., and **L. H. Frederickson.** 1986. Molt of female Lesser Scaup immediately following breeding. Auk 103: 293-298.

Austin, J. E., C. M. Custer, and **A. D. Afton.** 1998. Lesser Scaup (*Aythya affinis*) *in* The birds of North America, Number 338. *Edited by* A. Poole and F. Gill. The American Ornithologists' Union, Washington D.C.

Austin, J. E., J. E., A. D. Afton, M. G. Anderson, R. G. Clark, C. M. Custer, J. S. Lawrence, J. B. Pollard, and **J. K. Ringleman.** 2000. Declining scaup populations: issues, hypotheses, and research needs. Wildlife Society Bulletin 28: 254-263.

Bart, J., and **D. S. Robson.** 1982. Estimating survivorship when the subjects are visited periodically. Ecology 63: 1078-1090.

Beauchamp, W. D., R. R. Koford, T. D. Nudds, R. G. Clark, and **D. H. Johnson.** 1996. Long-term declines in nest success of prairie ducks. Journal of Wildlife Management 60: 247-257.

Blums, P., J. D. Nichols, J. E. Hines, and **A. Mednis.** 2002. Sources of variation in survival and breeding site fidelity in three species of European ducks. Journal of Animal Ecology 71: 438-450.

Brook, R. W. 2002. Breeding ecology and local population dynamics of Lesser Scaup (*Aythya affinis*) in boreal forest of western Canada. M.Sc. thesis, University of Saskatchewan, Saskatoon, Canada.

Brook, R. W., and **R. G. Clark.** 2002. Retention and effects of nasal markers and subcutaneously implanted radio transmitters on breeding female Lesser Scaup. Journal of Field Ornithology 73: 206-212.

Burnham, K. P., and **D. R. Anderson.** 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, USA.

Cowardin, L. M., D. S. Gilmer, and **C. W. Shaffer.** 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildlife Monographs 92.

Custer, C. M., T. W. Custer, and **D. W. Sparks.** 1996. Radio telemetry documents 24-hour feeding activity of wintering Lesser Scaup. Wilson Bulletin 108: 556-566.

Dawson, R. D., and **R. G. Clark.** 1996. Effects of variation in egg size and hatching date on survival of Lesser Scaup *Aythya affinis* ducklings. Ibis 138: 693-699.

Dawson, R. D., and **R. G. Clark.** 2000. Effects of hatching date and egg size on growth, recruitment and adult size of Lesser Scaup. Condor 102: 930-935.

Dwyer, C. P., and **G. A. Baldassarre.** 1993. Survival and nest success of sympatric female Mallards, *Anas platyrhynchos*, and American Black Ducks, *A. rubripes*, breeding in a forested environment. Canadian Field-Naturalist 107: 213-216.

Dzus, E. H., and **R. G. Clark.** 1998. Brood survival and recruitment of Mallards in relation to wetland density and hatching date. Auk 115: 311-318.

Flint, P. L., K. H. Pollock, D. Thomas, and **J. S. Sedinger.** 1995. Estimating prefledging survival: allowing for brood mixing and dependence among brood mates. Journal of Wildlife Management 59: 448-455.

Fournier, M. A., and **J. E. Hines.** 2001. Breeding ecology of sympatric Greater and Lesser Scaup (*Aythya marila* and *Aythya affinis*) in the subarctic Northwest Territories. Arctic 54: 444-456.

Fox, G. A., and **J. Gurevitch.** 2000. Population numbers count: tools for near-term demographic analysis. American Naturalist 156: 242-256.

Garrettson, P. R., T. J. Moser, and **K. A. Wilkins**. 2003. U.S. Fish and Wildlife Service: Waterfowl Population Status, 2003. U.S. Department of the Interior, Washington, D.C.

Gollop, J. B., and **W. H. Marshall.** 1954. A guide for aging duck broods in the field. Mississippi Flyway Technical Council (mimeo).

Grand, J. B., and **P. L. Flint.** 1996. Survival of Northern Pintail ducklings on the Yukon-Kuskokwim Delta, Alaska. Condor 98: 48-53.

Graybill, F. A., and **H. K. Iyer.** 1994. Regression analysis: concepts and applications. Duxbury Press, Belmont, USA.

Guyn, K. L., and **R. G. Clark.** 1999. Factors affecting survival of Northern Pintail ducklings in Alberta. Condor 101: 369-377.

Hammell, G. S. 1973. The ecology of the Lesser Scaup (*Aythya affinis Eyton)* in southwestern Manitoba. M.Sc. thesis, University of Guelph, Guelph, Ontario.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96: 651-661.

Johnson, D. H., J. D. Nichols, and **M. D. Schwartz.** 1992. Population dynamics of breeding waterfowl. Pages 446-485 *in* Ecology and Management of Breeding Waterfowl. *Edited by* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankeny, D. H. Johnson, J. A. Kadlec, and G. L. Krapu. University of Minnesota Press, Minneapolis, USA.

Kirby, R. E., and **L. M. Cowardin.** 1986. Spring and summer survival of female Mallards from northcentral Minnesota. Journal of Wildlife Management 50: 38-43.

Klett, A. T., H. F. Duebbert, C. A. Faanes, and **K. F. Higgins.** 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. U.S. Fish and Wildlife Service Resource Publication 158. 24 pages.

Koons, D. N. 2001. Lesser Scaup breeding ecology in the Canadian parklands. M.S. thesis, Montana State University, Bozeman, USA.

Koons, D. N., and **J. J. Rotella.** 2003. Comparative nesting success of sympatric Lesser Scaup and Ring-necked Ducks. Journal of Field Ornithology 74: 222-229.

Livezey, B. C. 1996. A phylogenetic analysis of modern Pochards (Anatidae: Aythini). Auk 113: 74-93.

Lokemoen, J. T., and **D. E. Sharp.** 1985. Assessment of nasal marker materials and designs used on dabbling ducks. Wildlife Society Bulletin 13: 53-56.

Machin, K. L., and **N. A. Caulkett.** 1998. Investigation of injectable anesthetic agents in Mallard ducks (*Anas platyrhynchos*): a descriptive study. Journal of Avian Medicine and Surgery 12: 255-262.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456-466.

McCullogh, P., and **J. A. Nelder.** 1989. Generalized linear models. Chapman & Hall, New York, USA.

Petrie, M. J., R. D. Drobney, and **D. T. Sears.** 2000. Mallard and Black Duck breeding parameters in New Brunswick: a test of the reproductive rate hypothesis. Journal of Wildlife Management 64: 832-838.

Ringleman, J. K., and **J. R. Longcore.** 1983. Survival of female Black Ducks *Anas rubripes*, during the breeding season. Canadian Field-Naturalist 97: 62-65.

Rogers, J. P. 1964. Effect of drought on reproduction of the Lesser Scaup. Journal of Wildlife Management 28: 213-222.

Rotella, J. J., and **Ratti, J. T.** 1992. Mallard brood survival and wetland habitat conditions in southwestern Manitoba. Journal of Wildlife Management 56: 499-507.

Rotella, J. J., M. L. Taper, and **A. J. Hansen.** 2000. Correcting nest success estimates for possible observer effects: maximum likelihood estimates of daily survival rates with reduced bias. Auk 117: 92-109.

Rotella, J. J., R. G. Clark, and **A. D. Afton.** 2003. Survival of female lesser scaup: effects of body size, age, and reproductive effort. Condor 105: 336-347.

Sargeant, A. B., R. J. Greenwood, M. A. Sovada, and **T. L. Shaffer.** 1993. Distribution and abundance of predators that affect duck production – prairie pothole region. United States Department of the Interior Fish and Wildlife Service Resource Publication 194.

Sayler, R. D. 1985. Brood parasitism and reproduction of Canvasbacks and Redheads on the Delta Marsh. Ph.D. dissertation, University of North Dakota, Grand Forks, USA.

Townsend, G. H. 1966. A study of waterfowl nesting on the Saskatchewan River Delta. Canadian Field Naturalist 80: 74-88.

Trauger, D. L. 1974. Eye color of female Lesser Scaup in relation to age. Auk 91: 243-254.

Weller, M. V. 1957. An automatic nest-trap for waterfowl. Journal of Wildlife Management 21: 456-458.

White, G. C., and **K. P. Burnham.** 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (supplement): S120-139.

Received 11 April 2002
Accepted 19 April 2004

Landscape Influence on *Canis* Morphological and Ecological Variation in a Coyote-Wolf *C. lupus* × *latrans* Hybrid Zone, Southeastern Ontario

HILARY J. SEARS[1, 3], JOHN B. THEBERGE[1,4], MARY T. THEBERGE[1,4], IAN THORNTON[1,5] and G. DOUGLAS CAMPBELL[2]

[1] School of Planning, Faculty of Environmental Studies, University of Waterloo, Waterloo, Ontario N2L 3G1 Canada
[2] Canadian Cooperative Wildlife Health Centre, Ontario Veterinary College, University of Guelph, Guelph, Ontario N1G 2W1 Canada; e-mail dgcampbe@uoguelph.ca
[3] Present address: R.R. 2, Brookfield, Nova Scotia B0N 1C0 Canada; e-mail downbythebay@ns.sympatico.ca; corresponding author Hilary J. Sears Paquet.
[4] Present address: R.R. 3, Site 25, Compartment 82, Oliver, British Columbia V0H 1T0 Canada; e-mail johnmarythe@telus.net
[5] Present address: Ontario Ministry of Natural Resources, 300 Water Street, Peterborough, Ontario K9J 8M5, Canada; e-mail ian.thorton@mnr.gov.on.ca

Sears, Hilary J., John B. Theberge, Mary T. Theberge, Ian Thornton, and G. Douglas Campbell. 2003. Landscape influence on *Canis* morphological and ecological variation in a Coyote-Wolf *C. lupus* × *latrans* hybrid zone, southeastern Ontario. Canadian Field-Naturalist 117(4): 591-600.

The ecology of Coyote-Wolf (*Canis latrans* × *C. lupus*) hybrids has never fully been typified. We studied morphological and ecological variation in *Canis* within a region of Coyote-Wolf hybridization in southeastern Ontario. We assessed *Canis* morphology from standard body measurements and ten skull measurements of adult specimens and found that *Canis* in this region are morphologically intermediate between Algonquin Provincial Park Wolves (*C. lupus lycaon*) and Coyotes, indicating a *latrans* × *lycaon* hybrid origin; however, there is a closer morphological affinity to *latrans* than *lycaon*. Analysis of 846 scats indicated dietary habits also intermediate between *lycaon* and Coyotes. We used a geographic information system (GIS) to assess spatial landscape features (road density, land cover and fragmentation) for six study sites representing three landscape types. We found noticeable variation in *Canis* morphology and diet in different landscape types. In general, canids from landscape type A (lowest road density, more total forest cover, less fragmentation) displayed more Wolf-like body morphology and consumed a greater proportion of larger prey (Beaver [*Castor canadensis*] and White-tailed Deer [*Odocoileus virginianus*]). In comparison, canids from landscape types B and C (higher road density and/or less total forest cover, more fragmentation) were generally more Coyote-like in body and skull morphology and made greater use of medium to small-sized prey (Groundhog [*Marmota monax*], Muskrat [*Ondatra zibethicus*] and lagomorphs). These landscape trends in *Canis* types suggest selection against Wolf-like traits in fragmented forests with high road density. The range of *lycaon* southeast of Algonquin Provincial Park appears to be limited primarily due to human access and consequent exploitation. We suggest that road density is the best landscape indicator of *Canis* types in this region of sympatric, hybridizing and unprotected *Canis* populations.

Key Words: Coyote, *Canis latrans*, Gray Wolf, *Canis lupus*, hybridization, road density, morphology, landscape influence, Ontario.

The objectives of this study were to assess potential relationships between landscape characteristics (e.g., road density, forest cover and fragmentation) and morphological and ecological variation in *Canis* in a Coyote-Wolf hybrid zone of southeastern Ontario. Coyote-Wolf (*Canis latrans* × *C. lupus*) hybridization (Lehman et al. 1991; Wilson et al. 1996) and intermediate-sized canids (Kolenosky and Standfield 1975; Nowak 1979; Schmitz and Kolenosky 1985; Schmitz and Lavigne 1987) have previously been described in eastern Ontario, an interface region between Wolf range in the north and Coyote range in the south (Kolenosky et al. 1978; Buss and de Almeida 1997). In parts of the Great Lakes region, spatial landscape features have been used to describe areas of favorable Wolf habitat (Thiel 1985; Jensen et al. 1986; Mech et al. 1988; Fuller et al. 1992; Mladenoff et al. 1995), but not in relation to Coyote-Wolf hybridization.

Habitat and landscape conditions have been implicated in the extirpation of wild Red Wolves (*C. rufus*) prior to 1970, the shrinkage of the range of *C. lupus lycaon* and coyote colonization in eastern North America (Nowak 1978; Moore and Parker 1992), as well as extensive *latrans-lycaon* and *latrans-rufus* hybridization (Lehman et al. 1991; Wayne and Jenks 1991; Roy et al. 1994). The study area on the Frontenac Axis of southeastern Ontario is characterized by a forested matrix ranging from landscapes of continuous forest and low road density, potentially suitable Wolf habitat (Thiel 1985; Jensen et al. 1986, Mech et al. 1988; Fuller et al. 1992; Mladenoff et al. 1995), to mixed forest-agricultural landscapes. It was hypothesized that *lycaon* would be found in continuously-forested landscapes similar to Algonquin Provincial Park to the north, and that Coyote-like animals would predominate in landscapes with less forest cover, more agricultural activity and higher road density.

This paper is relevant to the conservation of the adjacent Algonquin Provincial Park *lycaon* population. *Lycaon*, which has lost over half its historic range (Nowak 1995), is considered a subspecies of Gray Wolf (Nowak 1995), or more recently, a separate species, *C. lycaon*

(Wilson et al. 2000). Algonquin Provincial Park may represent one of few core *lycaon* populations remaining. The influence of hybridization on the Algonquin *lycaon* population (Wilson et al. 1996) is of concern; this study will describe conditions favoring hybridization.

Study Area

Regional Setting

The study was conducted from 1996 to 1998 in southeastern Ontario within a 10 000 km^2 region centered (45°15'N, 77°W) approximately 80 km southeast of Algonquin Provincial Park (Figure 1). Topography varies from lowland flats of the Ottawa Valley to upland, rolling terrain of the Madawaska Highlands. Elevations range from approximately 150 m to 450 m. The area contains several large lakes and rivers, and wetlands are common. Mean daily July and January temperatures are about 19°C and -11°C, respectively. Mean annual precipitation ranges from 65 cm in the north to 90 cm in the southwest, and mean annual snowfall is 200 cm (Brown et al. 1968).

Most of the study area lies on the Frontenac Axis, or Frontenac Arch, part of the Precambrian rock of the Canadian Shield which extends from southeastern Ontario to upper New York State (Douglas 1976; Davidson 1988). Frontenac Axis physiography makes much of the study region unsuitable for agriculture; consequently, extensive portions remain forested and with low human population, although farms, communities and small towns are scattered throughout the region. The Axis is recognized as a link or corridor between the relatively undisturbed landscapes of Algonquin Provincial Park in Ontario and Adirondack State Park in New York (Keddy 1995). Highway 7, demarcating the lower third of the Ontario portion of the Axis, was used as the approximate southern boundary of the study region; south of the highway is much greater human settlement, higher road density and more agricultural activity. Approximately half of the study region has an all-season road density less than 0.6 km/km^2 (Buss and de Almeida 1997: Figure 4), and a considerable amount of the central Frontenac region is public land (Keddy 1995: Figure 7).

The study region is almost entirely within the Middle Ottawa section of the Great Lakes-St. Lawrence forest region (Rowe 1972). Common upland species include Sugar Maple (*Acer saccharum*), Beech (*Fagus grandifolia*), Yellow Birch (*Betula alleghaniensis*), Red Maple (*A. rubrum*), Eastern Hemlock (*Tsuga canadensis*), Eastern White Pine (*Pinus strobus*) and Red Pine (*P. resinosa*). Also occurring are White Spruce (*Picea glauca*), Balsam Fir (*Abies balsamea*), Trembling Aspen (*Populus tremuloides*), White Birch (*B. papyrifera*), Red Oak (*Quercus rubra*) and Basswood (*Tilia americana*). Common species in lowlands and wet areas include Eastern White Cedar (*Thuja occidentalis*), Tamarack (*Larix laricina*), Black Spruce (*Picea mariana*), Black Ash (*Fraxinus nigra*), Red Maple and White Elm (*Ulmus americana*).

When this research was conducted, *Canis* in this region were legally protected only in Algonquin Provincial Park (7571 km^2) and from December 15 to March 31 in three townships adjacent to the southeast corner of the Park. An estimated 150-200 Wolves in approximately 36-38 packs are found in Algonquin Park (J. Theberge, unpublished data). Canid densities are not known for the Frontenac region or most of the remainder of the province (Buss and de Almeida 1997). Wolves, Coyotes, and their hybrids are classed as fur-bearing animals in Ontario and can be hunted or trapped in the southern part of the province throughout the year with a small-game hunting license or trapping license, with no bag limits or quotas (Buss and de Almeida 1997).

Study Sites

Six landscapes (sites; Figure 1) averaging about 230 km^2 were selected to represent one of three *relative* landscape types: A (low road density, high percent forest cover, low fragmentation), B (moderate road density, moderate percent forest cover, moderate fragmentation), and C (high road density, low percent forest cover, high fragmentation; Table 2).

The Dacre and Grimsthorpe sites represented parts of the most continuously-forested areas on the Frontenac Axis. The Dacre site (Renfrew County), 180 km^2, is in the Madawaska Highlands, immediately east of highway 41 between the communities of Griffith and Dacre, and north of Centennial and Black Donald Lakes. The Grimsthorpe site (Hastings County and Lennox and Addington County), 246 km^2, is between highways 41 and 62, immediately west of Bon Echo Provincial Park and Skootamatta Lake and immediately north of Lingham Lake. The Dacre site has few permanent residences and Grimsthorpe has none, but both have several recreational or hunt camps. Most of the land in these two sites is public land with fairly extensive networks of logging roads.

The Millbridge site (Hastings County), 143 km^2, is located on highway 62 between the towns of Madoc and Bancroft. The Admaston site (Renfrew County), 196 km^2, is west of the town of Renfrew and south of highway 5. The Lanark site (Lanark County), 322 km^2, lies immediately east of highway 511 and north of the town of Lanark. The Lake Clear site (Renfrew County), 278 km^2, is between Lake Clear and Golden Lake, immediately east of highway 512 and west of the town of Eganville. Approximately 80 to 90% of the land in these four sites is privately owned, with quite extensive networks of regional and concession roads. Active and/or abandoned farmlands are common.

Prey Base

Mammals found in the study area include White-tailed Deer (*Odocoileus virginianus*), Beaver (*Castor canadensis*), Muskrat (*Ondatra zibethicus*), Fisher

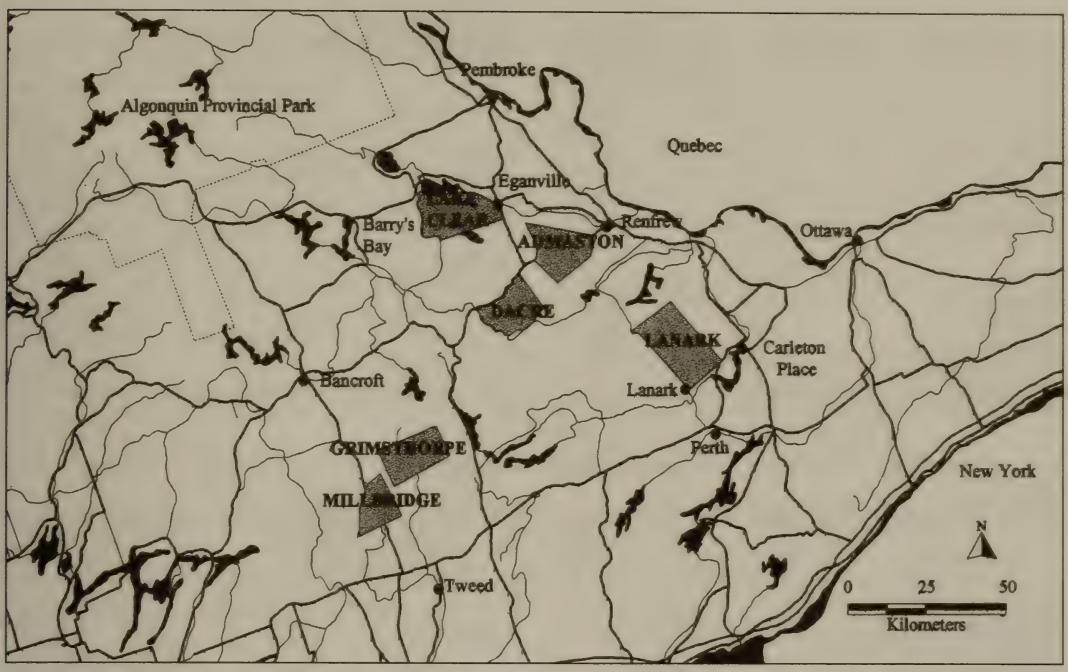


FIGURE 1. Six study sites (shaded polygons) in the Frontenac Axis region of southeastern Ontario.

(*Martes pennanti*), Marten (*Martes americana*), Raccoon (*Procyon lotor*), Groundhog (*Marmota monax*), Red Fox (*Vulpes vulpes*) and Black Bear (*Ursus americanus*), as well as smaller mammals including Snowshoe Hare (*Lepus americanus*), Eastern Cottontail (*Sylvilagus floridanus*), Mink (*Mustela vison*), Eastern Chipmunk (*Tamias striatus*) and numerous species of microtine rodents (Dobbyn 1994). Parts of the study region and individual sites are recognized as Deer wintering areas (Ontario Ministry of Natural Resources [OMNR] unpublished data). Moose (*Alces alces*), at the southern edge of their range in Ontario, occur at very low densities ($\leq 0.03 - 0.05$ Moose/km^2) in the study region (OMNR 1997; OMNR unpublished data, 1995-1996 and 1996-1997 aerial surveys) and are likely the only wild prey species not common in all sites. Domestic livestock are present in all sites except Dacre and Grimsthorpe; carcasses were used as bait for *Canis* by hunters in some other sites, making it difficult to use scat analysis to distinguish direct livestock predation from carrion or bait feeding.

Methods

Landscape Assessment

Roads were digitized from recent (1987 – 1996) Natural Resources Canada 1:50 000 topographic maps using ARC/INFO 7.2.1 (Environmental Systems Research Institute [ESRI], Redlands, California) and classed into two categories: (1) all-season roads including all public, paved and unpaved roads passable year-round by two-wheel-drive vehicle; and (2) seasonal roads and trails (not necessarily open to public use) including unpaved, unimproved roads, forestry roads, trails and rail-trails. Site area and linear road distance (i.e., sum of lengths of roads) were summarized using ARCVIEW 3.1 (ESRI, Redlands, California) and used to calculate two road densities for each site: (1) all-season roads, and (2) all-season roads, seasonal roads and trails. Seasonal roads were included in this study, unlike others (Thiel 1985; Mech et al. 1988; Fuller et al. 1992; Mladenoff et al. 1995), as an indication of potential human access by four-wheel-drive vehicles, all-terrain vehicles and snowmobiles.

Land cover was determined for each site from remote sensing images (Landsat Thematic Mapper) at 25 m resolution from August 1996 (Lake Clear) and May 1996 (all other sites). Images were classified into 11 land cover classes (12 for Lake Clear; Table 1) using a minimum polygon size of 12 500 m^2. Due to considerable cloud cover over part of the Millbridge site, landscape assessment was based on a smaller, but typical area. Large cloud-shadow polygons in Lake Clear were excluded. Because a section of the Grimsthorpe site was affected by haze, making many forested areas appear as field and scrub vegetation, polygons there were manually re-classified to forest classes based on elevations: deciduous forest at higher elevations, wetlands or coniferous forest at lower elevations.

Landsat data were converted to ARC/INFO coverages, and FRAGSTATS*ARC 2.0.3 (Innovative GIS Solutions Inc., Fort Collins, Colorado) was used to summarize land cover classes and to calculate land-

TABLE 1. Comparison of standard body measurements of Frontenac *Canis* to Algonquin Park Wolves.

Measurement	Frontenac *Canis* Mean ± SE	n	Algonquin Wolf Mean ± SE	n
Male				
body mass (kg)	20.5 ± 0.6	27	30.3 ± 0.6	48
total length (cm)	139.3 ± 1.5	28	163.8 ± 1.4	47
foreleg length (cm)	36.9 ± 0.4	28	41.4 ± 0.4	42
hind foot length (cm)	21.5 ± 0.3	28	24.7 ± 0.3	47
Female				
body mass (kg)	17.5 ± 0.5	24	23.9 ± 0.6	40
total length (cm)	133.5 ± 1.7	26	154.3 ± 1.4	39
foreleg length (cm)	34.6 ± 0.5	24	39.0 ± 0.5	30
hind foot length (cm)	20.5 ± 0.3	24	23.3 ± 0.3	36

TABLE 2. Road density, land cover and landscape measures for two study sites for each of three landscape types in southeastern Ontario.

	Landscape Type A		Landscape Type B		Landscape Type C	
	Dacre	Grimsthorpe	Millbridge	Admaston	Lanark	Lake Clear
Road Density (km/km^2)						
All-season roads	0.01	0	0.33	0.50	0.64	0.65
Seasonal roads and trails	0.46	0.38	0.25	0.19	0.29	0.34
All roads and trails	0.47	0.38	0.58	0.69	0.93	0.99
Land Cover (% of landscape)						
Water	3.3	5.0	1.5	2.1	4.6	1.6
Wetland	1.1	4.1	3.2	1.6	3.2	3.2
Wetland, forested wetland	6.6	5.9	7.7	4.6	8.5	14.7
Lowland coniferous	50.4	19.4	20.1	24.3	16.9	27.2
Dense/mixed coniferous	22.9	31.8	24.7	30.9	18.3	18.9
Lowland/mixed deciduous	9.4	21.0	19.4	17.9	20.7	11.1
Upland deciduous	1.7	8.8	19.9	4.1	14.2	2.7
Scrub vegetation	1.8	2.4	1.4	3.6	3.8	5.5
Field	2.4	1.3	1.6	9.9	7.6	13.0
Road, rock, bare soil	0.3	0.3	0.4	0.8	1.2	2.0
Bare sandy soil	0.1	0.1	0.1	0.3	0.7	0.1
Quarry, surface mine	–	–	–	–	0.5	–
Landscape Measures						
Total area (ha)	17,361.8	23,397.1	13,469.0	18,553.4	30,566.4	26,015.3
Largest patch index (%)	35.7	3.3	3.6	2.6	2.3	2.6
Mean patch size (ha)	12.7	8.6	7.6	8.1	7.3	7.6
Patch density (#/100 ha)	7.9	11.6	13.2	12.3	13.7	13.1
Mean shape index	2.3	2.2	2.3	2.3	2.2	2.3
Area-weighted mean shape index	14.3	5.5	4.2	4.3	3.4	3.9
Simpson's diversity index	0.68	0.80	0.81	0.80	0.86	0.83

scape indices for each site. These indices were (1) total area of each site, (2) largest patch index (percentage of site occupied by largest patch), (3) mean patch size, (4) patch density (number of patches per 100 ha), (5) mean shape index (a measure of average perimeter-to-area ratio for all patches in the site), (6) area-weighted mean shape index (a measure of average perimeter-to-area ratio which gives more weight to large patches in the site by multiplying by the proportion of the site covered by each patch), and (7) Simpson's diversity index (a measure of the probability that any two randomly selected patches would be different land cover classes) (Table 2). These indices are described by McGarigal and Marks (1995).

The location of each Frontenac *Canis* specimen (see below) that did not fall within one of the six sites was assigned to one of the three landscape types based on a similar, but more general landscape assessment of a 250 km^2 (approximate) area centered on the known or approximate kill site. Road density and percent forested

versus non-forested land were estimated for each of these kill areas through examination of topographic maps, OMNR district maps, classified land cover data and familiarity with the areas.

Body and Skull Morphology Assessments

Frontenac *Canis* body morphology was evaluated from carcasses of 51 adult specimens collected from trappers and hunters in the study region during winters (December to March) 1995-1996 through 1997-1998 and from six adult animals live-trapped during summer 1998. Carcass collection focused on the six sites; the location of all specimens was known within at least a few kilometres. Noted during necropsy of carcasses, or during examination of live-captures in the field, were sex, body mass, total body length (including tail), foreleg length (from the elbow, the obvious notch on the back side of the leg just below the chest, to the end of the foot pad on the longest toe [not including the nail], measured along the back side and following contours) and hind foot length. Frozen carcasses were thawed before measurements were taken. Unskinned body mass (BM) of skinned carcasses was estimated from their skinned body mass (SBM) using the regression $BM = 0.97\ SBM + 4.56$ ($r^2 = 0.91$, $n = 8$ specimens for which both unskinned and skinned mass were known). The six live-captured animals were classed as more than 13 months old adult based on general tooth-wear patterns examined in the field (Bowen 1982; Landon et al. 1998). Other specimens were aged by Matson's Laboratory, Inc., Milltown, Montana, using cementum layer analysis of a lower canine tooth (Linhart and Knowlton 1967; Landon et al. 1998). Specimens at least one year old were considered adults; however, the actual minimum age was approximately 20 months since specimens were killed after December.

Body measurements were subjected to multivariate cluster analysis (SAS) to determine morphologically-similar groups (classes) of individuals which were then compared to landscape type. MANOVA (SAS) was used to determine if significant differences existed among the body size classes. Frontenac *Canis* body measurements were compared using a Student's t-test with existing data on live-trapped or hunter/trapper-killed adult Algonquin Park Wolves obtained between 1987 and 1997 (Theberge et al. 1996; J. Theberge, unpublished data). Frontenac *Canis* body morphology was also compared generally to Eastern Coyote morphology reported in the literature.

Skull measurements and analyses followed those of Nowak (1995). Ten skull measurements were taken with calipers and recorded to the nearest 0.5 mm: (1) greatest skull length, (2) zygomatic width, (3) alveolar length from P1 to M2, (4) maximum width across outer sides of P4, (5) palatal width between alveolar of P1, (6) width of frontal shield, (7) height from alveolar of M1 to most ventral point of orbit, (8) depth of jugal, (9) crown length of P4, and (10) crown width of M2. Linear discriminant analysis was used to determine possible trends in Frontenac skull morphology in relation to landscape type. Frontenac *Canis* skulls (26 male, 19 female) were considered "unknowns" and compared as individuals to three "known" groups of adult skulls: southwestern Ontario Coyotes (17 male, 23 female; OMNR collection 1958-1970), Adirondack Coyotes (9 male, 8 female; R. Chambers collection 1997 and 1998) and Algonquin Park Wolves (13 male, 12 female; 1989 to 1996; S. Stewart 1996*). Each Frontenac specimen was assigned to the group which it most resembled morphologically based on its statistical distance (Mahalanobis' distance, D^2) from the groups.

Because of incomplete carcasses and damaged skulls, Frontenac specimens used in multivariate body and skull analyses represented a sub-sample of all adult specimens collected during this study.

Diet Assessment

Frontenac *Canis* diet was assessed from 846 scats (479 summer, 367 winter) collected from May to August 1996 and throughout May 1997 and August 1997 along unpaved roads and trails throughout the six sites. Scats were classed by season (summer or winter) based on estimated age at date of collection. Old scats collected in May represented diet from the previous winter; scats deposited in May through August represented summer diet. Scats were heated in an autoclave at 120°C and 125 kPa for 20 minutes. Three hairs were randomly chosen from each scat and identified microscopically by scale patterns and pigment patterns of the medulla (Adorjan and Kolenosky 1969) and by comparison to a reference collection. Selection of a fourth hair results in an additional prey species in less than 3% of Algonquin Wolf scats (Swanson 1989), therefore three hairs were considered sufficient. Percent frequency of occurrence was considered as the number of occurrences of each mammalian prey type expressed as a percentage of the total number of hairs analyzed for each site and season. Percent frequency of occurrence was used to indicate relative amounts of prey consumed in various landscapes and to allow direct comparison to the Forbes and Theberge (1996) study which used the same analysis for Algonquin Wolf diet (three hairs per scat, percent frequency of occurrence). For each season, a chi-square analysis on a contingency table (using number of hairs rather than percent frequency of occurrence) was used to test the null hypothesis that there was no difference in mammalian prey consumed among sites. Some prey types were combined in the chi-square analysis to ensure that no more than 20% of the expected cell frequencies were less than five (Owen and Jones 1990); Moose and Cow were excluded since they were not available in all sites. Non-mammalian prey items were recorded on a presence/absence basis in each scat. Conclusions about food habits are limited in Lake Clear and Admaston because few scats were found ($n = 30$ and $n = 51$, respectively).

Results

Hybrid Position of Frontenac Canis

In general, Frontenac canids were intermediate between Algonquin Wolves and Coyotes in body morphology. On average, Frontenac canids were significantly smaller than Algonquin Wolves in all body measurements ($p < 0.001$ males, $p < 0.001$ females; Table 1). Frontenac *Canis* were considerably heavier than the average body mass reported for adult Eastern Coyotes throughout most of their range (males about 12.5 – 17 kg, females about 11 – 15 kg; e.g., Richens and Hugie 1974; Lorenz 1978; Moore and Millar 1986; Poulle et al. 1995). Coyotes from New Hampshire (males 20.3 kg, females 18.0 kg; Silver and Silver 1969) and Vermont (males 17.8 kg, females 16.4 kg; Person 1988) are closer in weight to Frontenac canids.

Description of Landscapes

Road densities and land cover summaries indicated increased human influence from type A to type C landscapes (Table 2). All-season road density was approximately 0 km/km^2 in landscape A, 0.33 and 0.50 km/km^2 in landscape B sites, and about 0.65 km/km^2 in landscape C. When all roads and trails were considered, density was considerably higher (0.38 – 0.99 km/km^2) in all landscape types. The highest proportions of forested land cover (coniferous and deciduous forest classes) were in landscape type A sites (Dacre 84.4%, Grimsthorpe 81.0%) and Millbridge (landscape type B, 84.1%); proportions were considerably lower in Admaston (landscape type B, 77.2%) and landscape type C sites (Lanark 70.1%, Lake Clear 59.9%). Millbridge was similar to landscape type A in total forest cover, but had a much higher road density.

Landscape indices revealed the expected trend of increased human disturbance (i.e., increased heterogeneity and fragmentation) from type A to type C (Table 2). Mean patch size was larger and patch density was lower in landscape A sites. Mean shape index values were similar for all sites. Area-weighted mean shape index values varied by landscape type, however, and indicated that large patches in all landscape types, but especially landscape type A sites, were more irregular (i.e., natural) in shape than small patches. The Simpson's diversity index values suggested greatest land-cover diversity in landscape type C sites.

Landscape Variation in Frontenac Canis

Five body size classes of Frontenac *Canis* were generated by multivariate cluster analysis for each sex (SAS; Table 3). Landscape type A was represented predominantly by canids with large body size (Figure 2a); 50% of 20 specimens from landscape type A were large-bodied specimens (size classes 4 and 5), although all male size classes and all except the smallest female size class were represented in landscape type A. Five (71%) of seven specimens from landscape type B were medium-sized specimens (classes 2 and 3), and all of the 21 specimens from landscape type C fit in small and medium body size classes (1, 2 and 3). The largest Frontenac specimens (size classes 4 and 5 combined) were significantly smaller (t-tests, $p < 0.05$) than Algonquin Wolves except in female foreleg length.

Frontenac *Canis* skull morphology was also more Wolf-like in landscape type A (Figure 2b) based on the linear discriminant analysis. Of 17 Frontenac *Canis* skulls from landscape type A, 9 (53%) most resembled Algonquin Wolves, 1 (6%) most resembled Adirondack Coyotes and 7 (41%) most resembled southwestern Ontario Coyotes. From landscape type B, 2 (15%) of the 13 Frontenac *Canis* specimens resembled Algonquin Wolves, 8 (62%) most resembled Adirondack Coyotes and 3 (23%) most resembled southwestern Ontario Coyotes. From landscape type C, 1 (6%) of the 15 Frontenac specimens was similar to Algonquin Wolves, 4 (27%) were most similar to Adirondack Coyotes and 10 (67%) were most similar to southwestern Ontario Coyotes.

Significant variation in diet was found among sites in both summer ($\chi^2 = 634.74$, df = 30, $p < 0.001$) and winter ($\chi^2 = 386.63$, df = 20, $p < 0.001$). Canids in landscape type A consumed large prey almost exclusively (Figure 3). Combined occurrences of Beaver and White-tailed Deer (adult and fawn) in scats from landscape A sites were 87.2% and 91.0% in summer and 82.6% and 86.3% in winter, considerably higher than landscape type B and C sites (34.4 – 50.0% in summer, 22.2 – 67.6% in winter). Fawn was a significant food item in all sites in summer and accounted for an average of 64% of all Deer occurrences in summer scats. In landscape types B and C, medium-sized prey (Groundhog, Muskrat and leporids) comprised a significant portion of the diet particularly in summer. Groundhog occurrence in summer scats corresponded closely to landscape type: < 2% in landscape A, 11.3 – 13.1% in landscape B and 23.0 – 27.8% in landscape C. Muskrat use was especially high in Millbridge (landscape B). Use of leporids and small mammals was low in most sites, but higher in landscapes B and C. Cow hair was found in scats from landscape types B and C; livestock and/or baiting was common in these sites. Non-mammalian prey items showed no obvious landscape trend, found in an average of 19.2% of summer scats (11.3 – 27.8% by site) and 4.6% of winter scats (2.7 – 8.7% by site). Fruit (*Rubus* spp., *Vaccinium* spp. and *Aralia* spp.) and grasses were the most common of these items. Insects, bird remains, garbage, eggshell, pine needles and buds occurred incidentally.

Discussion

Evidence of Intermediate Wolf/Coyote Characteristics

Frontenac *Canis* appear to hold an intermediate position between Eastern Coyotes and Algonquin Wolves in body size, skull morphology and diet, suggesting a *latrans-lycaon* hybrid origin. These results support previous morphological studies which described intermediate-sized canids in southeastern Ontario and suggest-

TABLE 3. Mean, minimum and maximum body measurements for five male (n = 26) and female (n = 22) classes of Frontenac *Canis* generated by multivariate cluster analysis (SAS).

		Body Mass (kg)			Total Length (cm)			Foreleg Length (cm)			Hind Foot Length (cm)		
Class[a]	n	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Male													
1	4	20.3	19.3	21.5	134.5	127.9	140.5	33.8	33.0	34.6	19.8	19.3	20.5
2	8	17.5	15.6	19.2	135.9	132.0	143.0	36.4	35.0	38.0	21.2	20.0	22.0
3	8	21.0	19.0	22.9	138.6	130.0	144.0	36.9	35.1	40.0	21.4	21.0	22.5
4	2	20.0	18.5	21.5	152.8	151.6	154.0	39.7	38.0	41.3	24.2	23.8	24.5
5	4	26.6	24.9	28.4	149.9	145.5	156.5	39.5	38.0	41.5	23.4	22.5	24.5
Female													
1	2	16.5	16.0	17.0	120.2	119.8	120.5	32.1	30.9	33.3	18.5	17.8	19.2
2	6	14.7	13.5	16.0	129.3	125.6	133.0	32.7	31.2	34.0	19.4	19.0	19.9
3	8	17.7	16.2	19.5	132.5	128.0	138.0	34.0	32.0	35.8	20.1	19.5	21.0
4	1	13.5	13.5	13.5	143.5	143.5	143.5	40.4	40.4	40.4	21.6	21.6	21.6
5	5	19.8	17.0	22.5	144.9	140.0	148.8	37.2	35.0	39.8	22.1	21.2	23.0

[a] Class 1 is smallest, 5 is largest (approximately); length measurements were given higher priority than body mass since it is subject to variation. These five classes accounted for 77% of the variation in male body size and 80% of the variation in female body size. Differences were significant among classes for both sexes (MANOVA, Wilk's Lambda Statistic, $p < 0.0001$).

ed a similar origin (Kolenosky and Standfield 1975; Nowak 1979; Schmitz and Kolenosky 1985). Our intermediate morphology and diet results are further supported by genetic analysis on the same Frontenac Axis specimens as were used for morphological analysis. Overall, allele frequencies of Frontenac *Canis* populations show them to be hybrids, but more similar to Coyotes in New Brunswick and New York State than to *lycaon* in Algonquin Provincial Park (A. Granacki, unpublished data).

The importance of White-tailed Deer in Frontenac *Canis* diet is consistent with the diet of both Wolves in the Great Lakes region (e.g., Pimlott et al. 1969; Van Ballenberghe et al. 1975; Voigt et al. 1976; Forbes and Theberge 1996) and Eastern Coyotes (e.g., Hilton 1976; Harrison and Harrison 1984; LaPierre 1985; Messier et al. 1986; Moore and Millar 1986; Parker 1986; Major and Sherburne 1987; Dibello et al. 1990; Samson and Crete 1997). However, the frequency of Groundhog, fruit and vegetation in Frontenac *Canis* summer scats is generally more characteristic of Eastern Coyotes (Hamilton 1974; Harrison and Harrison 1984; LaPierre 1985; Moore and Millar 1986; Parker 1986; Major and Sherburne 1987; Brundige 1993; Samson and Crete 1997) than Wolves in Algonquin Provincial Park and central Ontario (Pimlott et al. 1969; Voigt et al. 1976; Forbes and Theberge 1996). In contrast, the high use of Beaver by Frontenac *Canis* (excluding the Lake Clear site) is greater than Beaver use by Eastern Coyotes (Hilton 1976; Brundige 1993; Samson and Crete 1997) and similar to Wolf diet in the Algonquin region (Voigt et al. 1976; Forbes and Theberge 1996). Considerable use of Muskrat in Millbridge is uncharacteristic of *Canis* diet in northeastern North America.

Landscape Correlates of Canis *Types*

The most significant aspect of this study is in finding regional variation in *Canis* that correlates with landscape characteristics. In type A landscapes on the Frontenac Axis, the least influenced by humans, large body size, more Wolf-like skull morphology and high use of large prey indicate that canids remain the most *lycaon*-like. Similarly, but to an even greater degree, Algonquin Wolves retain morphological, behavioural and dietary traits typical of Wolves (Theberge et al. 1996) despite the introgression of Coyote mtDNA in the population (Lehman et al. 1991; Wilson et al. 1996), suggesting continued selection for Wolf-like characteristics in the Algonquin landscape. In contrast, in more disturbed Frontenac landscapes, smaller body size, more Coyote-like skull morphology and varied diet suggest selection for Coyote-like characteristics. The body morphology of small body size classes (Table 3) is comparable to measurements reported by Lorenz (1978) for New England Coyotes (average total lengths of 125.8 cm [range 112 – 137 cm] and 120.4 cm [110 – 151 cm], and hind foot lengths of 19.9 cm [17.8 – 21.6 cm] and 19.0 cm [17.8 – 22.2 cm] for males and females, respectively). The diverse diet with a greater proportion of medium to small prey in landscape types B and C is similar to Eastern Coyote diet in areas with farmland and/or non-forested land (Hilton 1976; Harrison and Harrison 1984; LaPierre 1985; Person 1988).

Preliminary genetic analyses of Frontenac *Canis* did not detect any distinct trend in genotypes in relation to landscape types (A. Granacki, unpublished data; S. Grewal, unpublished data). Landscape type A had the highest percentage of specimens with the most *lycaon*-like genotypes (36% of 14 specimens) based

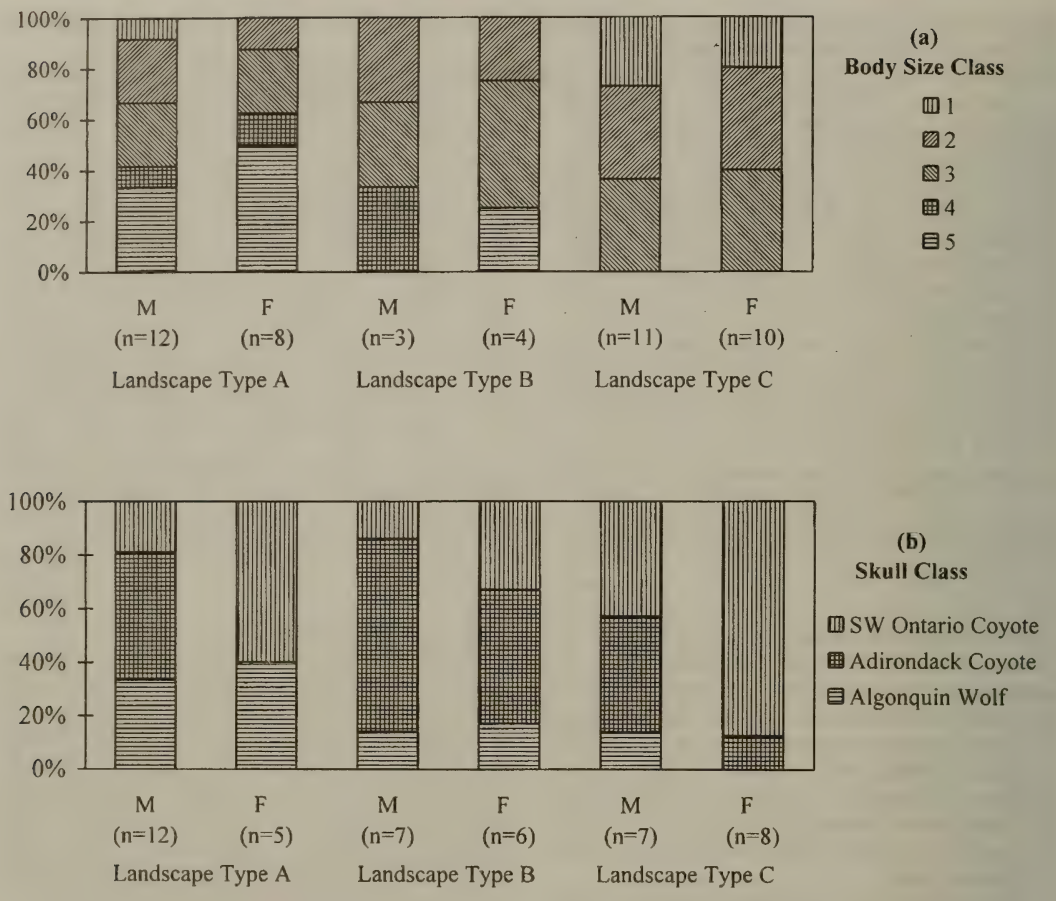


FIGURE 2 (a) Percent of male (M) and female (F) Frontenac *Canis* from each landscape type (A, B, C) in five body size classes (Class 1 is smallest, 5 is largest; see Table 3) based on cluster analysis, and (b) Percent of Frontenac *Canis* skulls from each landscape type that most resembled southwestern Ontario Coyotes, Adirondack Coyotes and Algonquin Wolves based on linear discriminant analysis. Frontenac *Canis* sample size for each landscape type is shown in parentheses.

on nuclear DNA analysis (A. Granacki 1998*). In landscape types B and C, 12% of 26 specimens and 26% of 39 specimens had *lycaon*-like genetic profiles, respectively. The percentages of Frontenac specimens from landscape types A, B and C with the most *latrans*-like genetic profiles were 29%, 35% and 28%, respectively.

Landscape differences in Frontenac *Canis* types suggest a hybridization scenario in southeastern Ontario similar to that involving *C. rufus* (Red Wolf) and *C. latrans* in the southeastern United States. As a result of human exploitation Red Wolves remained only in isolated areas of the southeastern United States (Gipson 1978). *Canis* with intermediate morphology (McCarley 1962; Riley and McBride 1975; Gipson 1978; Nowak 1979) and Coyote genotypes (Wayne and Jenks 1991; Roy et al. 1994) were documented when Red Wolves and Coyotes hybridized between about 1930 and the 1970s. The sequence of Red Wolf extirpation and occurrence of *rufus-latrans* hybrids indicated that hybridization between Red Wolves and Coyotes occurred last where habitat changes were least (Riley and McBride 1975; Nowak and Federoff 1996). The most Red Wolf-like skulls from Oklahoma, for example, were from areas last to be extensively influenced by human activities (McCarley 1962).

The variation in canid types described in southeastern Ontario landscapes could result from a selective influence of differences in forest conditions, differences in prey, or differences in degree of human exploitation. The data described here and results of other studies provide little evidence that variation is due to habitat selection for different forest conditions; i.e., habitat choice by Wolf-like canids for more-forested habitat

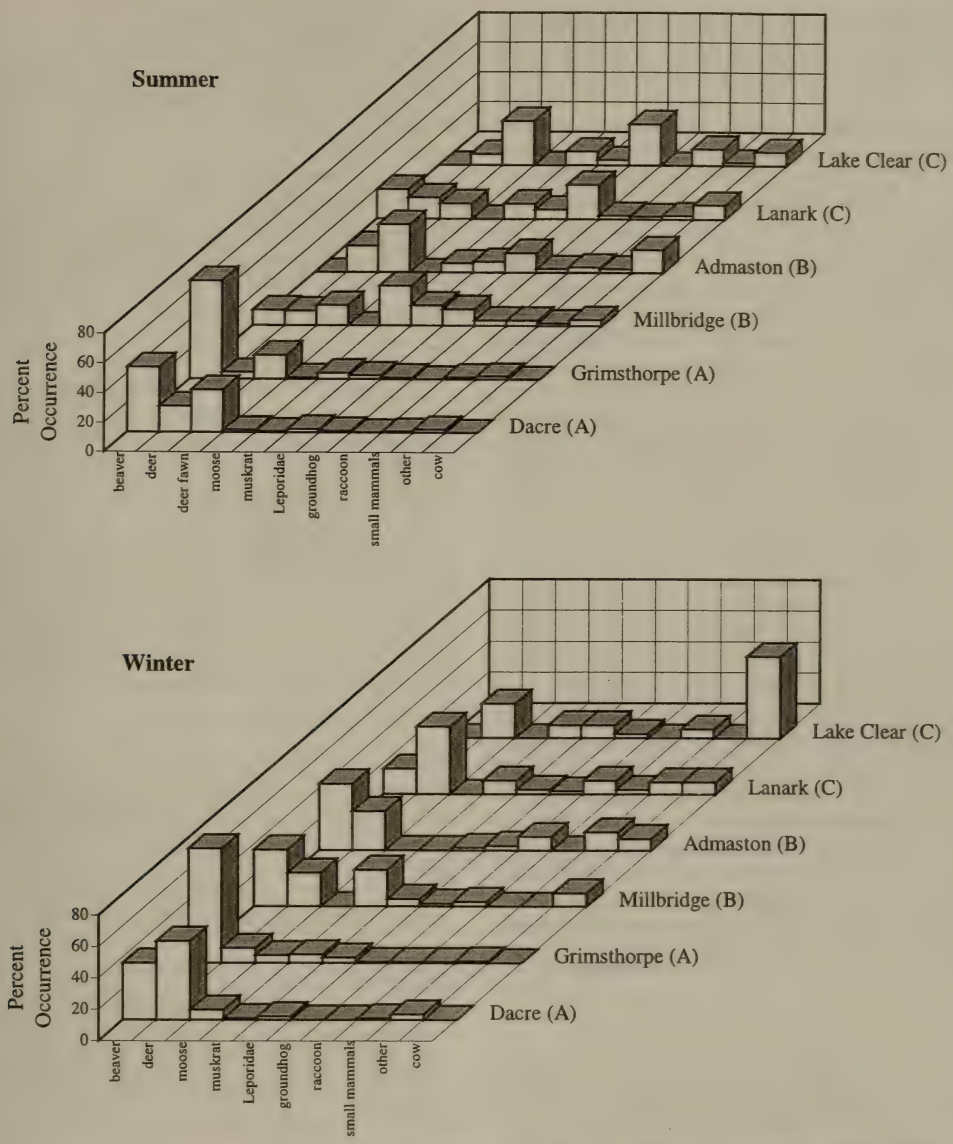


FIGURE 3. Variation in Frontenac *Canis* diet among six sites and three landscape types (A, B, C) in southeastern Ontario, based on percent frequency of occurrence of mammalian prey items in summer scats (Moose includes adult and calf) and winter scats.

and by Coyote-like canids for less-forested habitat. Wolves can inhabit open and semi-wild landscapes (Mladenoff et al. 1995; Mladenoff et al. 1997) and, conversely, Eastern Coyotes occupy closed forests (Parker 1986; Major and Sherburne 1987; Samson and Crete 1997).

Natural selection could operate to favour larger Wolf-like canids where prey are larger, and smaller ones where prey are smaller, as suggested in previous studies of Ontario *Canis* (Kolenosky and Standfield 1975; Schmitz and Kolenosky 1985; Schmitz and Lavigne 1987). However, differences in Frontenac *Canis* body size (Table 3) seem too slight to be selected for by differences in prey size. Regarding use of large prey, Moose were almost absent from the diet in all three landscape types, whereas deer were used in all landscape types. Regarding use of smaller prey, small and medium-sized prey were utilized more in landscapes types B and C, but deer were also important in these landscapes (e.g., Lanark had a high proportion [43%] of deer in winter scats).

Road density, as an index of human activity, access and exploitation, might be the single-most useful indicator of *Canis* type where there are sympatric, hybrid-

izing populations of *lycaon* and *latrans*. Higher Wolf mortality due to hunting and trapping has previously been reported in areas of higher road density where Wolves are not protected (Person et al. 1996). Our results suggest that the degree of human-caused selection through exploitation favors more Coyote-like canids. In landscape type C, where Coyote-like animals predominated, all-season road density was highest at approximately 0.65 km/km^2. In contrast, the most *lycaon*-like *Canis* were generally found in landscapes with lower all-season road density (i.e., approaching 0 km/km^2) and relatively low density of all roads and trails (i.e., about 0.4 km/km^2). In none of these sites are there any restrictions on the use of roads, like there are in Algonquin Provincial Park where *lycaon* exhibits predominantly Wolf-like morphology and behavioural characteristics (Theberge et al. 1996).

In eastern North America, Coyotes tended to expand into regions where Wolf populations declined (Gier 1975). Coyotes and hybrids have been found along the margins of the former range of *rufus* populations in the southeastern United States (Nowak and Federoff 1998) and along the southern edge of *lycaon* range in Ontario (Kolenosky and Standfield 1975; Schmitz and Kolenosky 1985). Exploitation produces conditions favoring *latrans-lycaon* hybridization within this region of sympatric, hybridizing and unprotected *Canis* populations in southeastern Ontario. In and near Algonquin Provincial Park, Coyotes appear to be progressively invading *lycaon* range by exploiting gaps in occupied range. The recent occurrence of some canids in Algonquin Provincial Park which are morphologically and genetically Coyote-like suggests that hybridization with Coyotes or hybrids is more likely in packs which have been fragmented, especially peripheral packs, primarily due to human-caused mortality (Theberge 1998: 256).

Conservation Implications

A road density of less than 0.6 km/km^2 has been described as necessary for wolf persistence in the Great Lakes region of the United States (Thiel 1985; Mech et al. 1988; Fuller et al. 1992; Mladenoff et al. 1995) where wolves are legally protected and populations are recovering (Mech 1995). This figure is not applicable as an indicator of *lycaon* distribution where wolves are not protected on the edge of their range in southeastern Ontario. Data from the Frontenac region suggest that the degree of human access through roads affects *Canis* types and that road densities even lower than 0.6 km/km^2 may limit persistence of *lycaon*. Although this study found little evidence of "pure" *lycaon* in the Frontenac region, presumably *lycaon* would be more likely to occur in landscapes similar to those described as type A in this study.

Management strategies for *Canis* where there is (or is potential for) Coyote-Wolf hybridization should consider low overall (i.e., all-season and seasonal) road density as the landscape feature most useful in predicting, and most critical in maintaining, the presence of Wolf-like canids or possibly Wolves. A road-density index lower than 0.6 km/km^2 appears to be particularly important where there is lack of protective status for canids and/or harvest seasons and bag limits. *Canis* management and *lycaon* conservation in southeastern Ontario should address the management and reduction of road access, for example through limiting construction of new roads, seasonally or permanently closing or gating roads, or rehabilitating seasonal roads after their primary function (e.g., forestry) is no longer required.

Acknowledgments

This project was funded by the Max Bell Foundation, World Wildlife Fund Canada and Wildlife Habitat Canada. We gratefully acknowledge the assistance provided by T. Bain, R. Chambers, L. Elliot, A. Granacki, S. Grewal, E. Harvey, J. Heal, B. Kelly, L. Lamb, D. Matthews, R. Nowak, S. Stewart, D. Voigt, B. White and P. Wilson. We thank the numerous trappers and hunters from southeastern Ontario who participated in this study and staff at the Ontario Ministry of Natural Resources offices at Bancroft, Carleton Place, Dacre, Pembroke and Tweed for their cooperation. We also thank the field assistants on the project, particularly L. Hunt and J. Schwartz.

Documents Cited (marked * in text)

Granacki, A. 1998. Microsatellite analysis of two Laurentian Highland canid populations outside of Algonquin Provincial Park. Undergraduate thesis, McMaster University, Hamilton, Ontario. 53 pages.

Stewart, S. 1996. Tooth and skull analysis of wolves (*Canis lupus*) from Algonquin Park, Ontario. Senior honours thesis, University of Waterloo, Waterloo, Ontario. 66 pages.

Literature Cited

Adorjan, A. S., and **G. B. Kolenosky.** 1969. A manual for the identification of hairs of selected Ontario mammals. Wildlife Resources Report Number 90, Research Branch, Ontario Department of Lands and Forests, Toronto, Ontario. 64 pages.

Bowen, D. W. 1982. Determining age of coyotes, *Canis latrans*, by tooth sections and tooth-wear patterns. Canadian Field-Naturalist 96: 339-341.

Brown, D. M., G. A. McKay, and **L. J. Chapman.** 1968. The climate of southern Ontario. Climatological Studies Number 5. Department of Transport, Meteorological Branch, Toronto, Ontario. 50 pages.

Brundige, G. C. 1993. Predation ecology of the eastern coyote, *Canis latrans* var., in the Adirondacks, New York. PhD thesis, State University of New York, Syracuse, New York.

Buss, M., and **M. de Almeida.** 1997. A review of wolf and coyote status and policies in Ontario. Ontario Ministry of Natural Resources. 88 pages.

Davidson, R. J. 1988. Foundations of the land – bedrock geology. Pages 36-47 *in* Legacy: the natural history of Ontario. *Edited by* J. B. Theberge. McClelland and Stewart Inc., Toronto, Ontario. 397 pages.

Dibello, F. J., S. M. Arthur, and **W. B. Krohn.** 1990. Food habits of sympatric coyotes, *Canis latrans*, red foxes, *Vulpes vulpes*, and bobcats, *Lynx rufus*, in Maine. Canadian Field-Naturalist 104: 403-408.

Dobbyn, J. (S.). 1994. Atlas of the mammals of Ontario. Federation of Ontario Naturalists, Don Mills, Ontario. 120 pages.

Douglas, R. J. W. 1976. Geology and Economic Minerals of Canada. Geological Survey of Canada, Department of Energy, Mines and Resources, Ottawa, Ontario.

Forbes, G. J., and **J. B. Theberge.** 1996. Response by wolves to prey variation in central Ontario. Canadian Journal of Zoology 74: 1511-1520.

Fuller, T. K., W. E. Berg, G. L. Radde, M. S. Lenarz, and **G. B. Joselyn.** 1992. A history and current estimate of wolf distribution and numbers in Minnesota. Wildlife Society Bulletin 20: 42-55.

Gier, H. T. 1975. Ecology and social behavior of the coyote. Pages 247-262 *in* The wild canids: their systematics, behavioral ecology and evolution. *Edited by* M. W. Fox. Van Nostrand Reinhold Co., New York, New York. 508 pages.

Gipson, P. S. 1978. Coyotes and related *Canis* in the southeastern United States with a comment on Mexican and Central American *Canis*. Pages 191-208 *in* Coyotes: biology, behavior, and management. *Edited by* M. Bekoff. Academic Press, New York, New York. 384 pages.

Hamilton, W. J., Jr. 1974. Food habits of the coyote in the Adirondacks. New York Fish and Game Journal 21: 177-181.

Harrison, D. J., and **J. A. Harrison.** 1984. Foods of adult Maine coyotes and their known-aged pups. Journal of Wildlife Management 48: 922-926.

Hilton, H. 1976. The physical characteristics, taxonomic status and food habits of the eastern coyote in Maine. MSc thesis, University of Maine, Orono, Maine. 66 pages.

Jensen, W. F., T. K. Fuller, and **W. L. Robinson.** 1986. Wolf, *Canis lupus*, distribution on the Ontario-Michigan border near Sault Ste. Marie. Canadian Field-Naturalist 100: 363-366.

Keddy, C. 1995. The conservation potential of the Frontenac Axis: linking Algonquin Park to the Adirondacks. Canadian Parks and Wilderness Society, Ottawa, Ontario. 59 pages.

Kolenosky, G. B. 1983. Status and management of wolves in Ontario. Pages 35-40 *in* Wolves in Canada and Alaska: their status, biology and management. *Edited by* L. N. Carbyn. Canadian Wildlife Service, Report Series Number 45.

Kolenosky, G. B., and **R. O. Standfield.** 1975. Morphological and ecological variation among gray wolves (*Canis lupus*) of Ontario, Canada. Pages 62-72 *in* The wild canids: their systematics, behavioral ecology and evolution. *Edited by* M. W. Fox. Van Nostrand Reinhold Co., New York, New York. 508 pages.

Kolenosky, G. B., D. R. Voigt, and **R. O. Standfield.** 1978. Wolves and coyotes in Ontario. Ontario Ministry of Natural Resources, Wildlife Branch. 19 pages.

Landon, D. B., C. A. Waite, R. O. Peterson, and **L. D. Mech.** 1998. Evaluation of age determination techniques for gray wolves. Journal of Wildlife Management 62: 674-682.

LaPierre, L. E. 1985. Fall and winter food habits of the eastern coyote *Canis latrans* in southeastern New Brunswick. Proceedings of the Nova Scotia Institute of Science 35: 71-74.

Lehman, N., A. Eisenhawer, K. Hansen, L. D. Mech, R. O. Peterson, P. J. P. Gogan, and **R. K. Wayne.** 1991. Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. Evolution 45: 104-119.

Linhart, S. B., and **F. F. Knowlton.** 1967. Determining age of coyotes by tooth cementum layers. Journal of Wildlife Management 31: 362-365.

Lorenz, J. R. 1978. Physical characteristics, movement and population estimate of the eastern coyote in New England. MSc thesis, University of Massachusetts. 62 pages.

Major, J. T., and **J. A. Sherburne.** 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. Journal of Wildlife Management 51: 606-616.

McCarley, H. 1962. The taxonomic status of wild *Canis* (Canidae) in the south central United States. The Southwestern Naturalist 7: 227-235.

McGarigal K., and **B. J. Marks.** 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General technical report PNW-GTR-351. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Mech. L. D. 1995. The challenge and opportunity of recovering wolf populations. Conservation Biology 9: 270-278.

Mech, L. D., S. H. Fritts, G. L. Radde, and **W. J. Paul.** 1988. Wolf distribution and road density in Minnesota. Wildlife Society Bulletin 16: 85-87.

Messier, F., C. Barrette, and **J. Huot.** 1986. Coyote predation on a white-tailed deer population in southern Quebec. Canadian Journal of Zoology 64: 1134-1136.

Mladenoff, D. J., T. A. Sickley, R. G. Haight, and **A. P. Wydeven.** 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conservation Biology 9: 279-294.

Mladenoff, D. J., R. G. Haight, T. A. Sickley, and **A. P. Wydeven.** 1997. Causes and implications of species restoration in altered ecosystems: a spatial landscape projection of wolf population recovery. BioScience 47: 21-31.

Moore, G. C., and **J. S. Millar.** 1986. Food habits and average weights of a fall-winter sample of eastern coyotes, *Canis latrans*. Canadian Field-Naturalist 100: 105-106.

Moore, G. C., and **G. R. Parker.** 1992. Colonization by the eastern coyote (*Canis latrans*). Pages 23-37 *in* Ecology and management of the eastern coyote. *Edited by* A. H. Boer. Wildlife Research Unit, University of New Brunswick, Fredericton, New Brunswick. 194 pages.

Nowak, R. M. 1978. Evolution and taxonomy of coyotes and related *Canis*. Pages 3-16 *in* Coyotes: biology, behavior and management. *Edited by* M. Bekoff. Academic Press, New York, New York. 384 pages.

Nowak, R. M. 1979. North American Quaternary *Canis*. Monograph Number 6, Museum of Natural History, University of Kansas, Lawrence, Kansas. 154 pages.

Nowak, R. M. 1995. Another look at wolf taxonomy. Pages 375-397 *in* Ecology and conservation of wolves in a changing world. *Edited by* L. N. Carbyn, S. H. Fritts, and D. R. Seip. Canadian Circumpolar Institute, Occasional Paper Number 35. University of Alberta, Edmonton, Alberta. 642 pages.

Nowak, R. M., and **N. E. Federoff.** 1996. Systematics of wolves in eastern North America. Pages 187-203 *in* Wolves of America conference proceedings, November 12-14, 1996, Albany, New York. Defenders of Wildlife, Washington, D. C. 306 pages.

Nowak, R. M., and **N. E. Federoff.** 1998. Validity of the red wolf: response to Roy et al. Conservation Biology 12: 722-725.

Ontario Ministry of Natural Resources. 1997. The Madawaska Highlands land use plan. 80 pages.

Owens, F. and **R. Jones.** 1990. Statistics. Third edition. Pitman, London, England. 480 pages.

Parker, G. R. 1986. The seasonal diet of coyotes, *Canis latrans*, in northern New Brunswick. Canadian Field-Naturalist 100: 74-77.

Person, D. K. 1988. Home range, activity, habitat use, and food habits of eastern coyotes in the Champlain Valley region of Vermont. MS thesis, University of Vermont, Burlington, Vermont. 103 pages.

Person, D. K., M. Kirchhoff, V. Van Ballenberghe, G. C. Iverson, and **E. Grossman.** 1996. The Alexander Archipelago wolf: a conservation assessment. General Technical Report PNW-GTR-384. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 42 pages.

Pimlott, D., J. Shannon, and **G. Kolenosky.** 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ontario Ministry of Natural Resources Report Number 87. 92 pages.

Poulle, M.-L., M. Crete, and **J. Huot.** 1995. Seasonal variation in body mass and composition of eastern coyotes. Canadian Journal of Zoology 73: 1625-1633.

Richens, V. B., and **R. D. Hugie.** 1974. Distribution, taxonomic status, and characteristics of coyotes in Maine. Journal of Wildlife Management 38: 447-454.

Riley, G. A., and **R. T. McBride.** 1975. A survey of the red wolf (*Canis rufus*). Pages 263-277 *in* The wild canids: their systematics, behavioral ecology and evolution. *Edited by* M. W. Fox. Van Nostrand Reinhold, New York, New York. 508 pages.

Rowe, J. S. 1972. Forest regions of Canada. Canadian Forestry Service Publication No. 1300. Department of Fisheries and the Environment. 172 pages.

Roy, M. S., E. Geffen, D. Smith, E. A. Ostrander, and **R. K. Wayne.** 1994. Patterns of differentiation and hybridization in North American wolflike canids, revealed by analysis of microsatellite loci. Molecular Biology and Evolution 11: 553-570.

Samson, C., and **M. Crete.** 1997. Summer food habits and population density of coyotes, *Canis latrans*, in boreal forests of southeastern Quebec. Canadian Field-Naturalist 111: 227-233.

Schmitz, O. J., and **G. B. Kolenosky.** 1985. Wolves and coyotes in Ontario: morphological relationships and origins. Canadian Journal of Zoology 63: 1130-1137.

Schmitz, O. J., and **D. M. Lavigne.** 1987. Factors affecting body size in sympatric Ontario *Canis*. Journal of Mammalogy 68: 92-99.

Silver, H., and **W. T. Silver.** 1969. Growth and behavior of the coyote-like canid of northern New England with observations on canid hybrids. Wildlife Monographs 17: 1-41.

Standfield, R. O. 1970. A history of timber wolf (*Canis lupus*) populations in Ontario, Canada. Pages 505-513 *in* Transactions of the 9th International Congress of Game Biology, Moscow, USSR.

Swanson, L. A. 1989. Migratory behavior and management of a white-tailed deer herd in Algonquin region, central Ontario. MA thesis, University of Waterloo, Waterloo, Ontario. 123 pages.

Theberge, J. B. 1998. Wolf country: eleven years tracking the Algonquin wolves. McClelland and Stewart, Inc., Toronto, Ontario. 306 pages.

Theberge, M. T., J. B. Theberge, G. J. Forbes, and **S. Stewart.** 1996. Is the Algonquin canid a wolf or a coyote? Pages 208-211 *in* Wolves of America conference proceedings, November 12-14, 1996, Albany, New York. Defenders of Wildlife, Washington, D.C. 306 pages.

Thiel, R. D. 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. American Midland Naturalist 113: 404-407.

Van Ballenberghe, V., A. W. Erickson, and **D. Byman.** 1975. The ecology of the timber wolf in northeastern Minnesota. Wildlife Monographs 43: 1-43.

Voigt, D. R., G. B. Kolenosky, and **D. H. Pimlott.** 1976. Changes in summer foods of wolves in central Ontario. Journal of Wildlife Management 40: 663-668.

Wayne, R. K., and **S. M. Jenks.** 1991. Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf *Canis rufus*. Nature 351: 565-568.

Wilson, P. J., S. Grewal, A. Sipek, J. B. Theberge, M. T. Theberge, and **B. N. White.** 1996. A molecular-genetic estimate of the extent of wolf-coyote hybridization in the wolf population of Algonquin Park, Ontario. Pages 204-207 *in* Wolves of America conference proceedings, November 12-14, 1996, Albany, New York. Defenders of Wildlife, Washington, D.C. 306 pages.

Wilson, P. J., S. Grewal, I. D. Lawford, J. N. M. Heal, A. G. Granacki, D. Pennock, J. B. Theberge, M. T. Theberge, D. R. Voigt, W. Waddell, R. E. Chambers, P. C. Paquet, G. Goulet, D. Cluff, and **B. N. White.** 2000. DNA profiles of the eastern Canadian wolf and the red wolf provide evidence for a common evolutionary history independent of the gray wolf. Canadian Journal of Zoology 78: 2156-2166.

Received 29 April 2002
Accepted 20 April 2004

Bald Eagles, *Haliaeetus leucocephalus*, Feeding on Spawning Plainfin Midshipman, *Porichthys notatus*, at Crescent Beach, British Columbia

KYLE HAMISH ELLIOTT[2], CHRISTINA L. STRUIK[1,2] and JOHN E. ELLIOTT[1,3]

[1]Canadian Wildlife Service, Pacific Wildlife Research Centre, 5421 Robertson Road, RR1 Delta, British Columbia V4K 3N2 Canada
[2]Vancouver Natural History Society, PO Box 3021, Vancouver, British Columbia V6B 3X5 Canada
[3]Corresponding author: john.elliott@ec.gc.ca.

Elliott, Kyle Hamish, Christina L. Struik, and John E. Elliott. 2003. Bald Eagles, *Haliaeetus leucocephalus*, feeding on spawning Plainfin Midshipman, *Porichthys notatus*, at Crescent Beach, British Columbia. Canadian Field-Naturalist 117(4): 601-604.

We observed Bald Eagles feeding on Plainfin Midshipman near Crescent Beach, British Columbia, in May and June 2001 and 2002. We quantified consumption rates and eagle numbers during this period, illustrating the potential importance of this food source to breeding eagles. Tide height was the only significant factor influencing consumption rates, likely because this variable reflected the availability of midshipman prey.

Nous avons observé les Pygargues à tête blanche alimenter sur les Crapauds à nageoire unie près de Crescent Beach, Colombie-Britannique, en maie et juin 2001 et 2002. Nous avons mesuré les cadences de consommation et les nombres de pygargues pendant cette période, illustrant l'importance potentielle de cette source de nourriture pour les aigles. La taille de marée était le seul facteur significatif influençant les cadences de consommation et les nombres de pygargues pendant la période d'étude, probablement parce que cette variable a reflété la disponibilité des crapauds.

Key words: Bald Eagle, *Haliaeetus leucocephalus*, foraging rates, Plainfin Midshipman, *Porichthys notatus*, British Columbia.

Bald Eagles (*Haliaeetus leucocephalus*) will travel thousands of kilometers from natal areas to congregate at large dependable food supplies (Servheen and English 1979; Buehler 2000). Well-known examples include annual congregations of eagles feeding on wintering waterfowl and spawning salmon and herring (Stalmaster 1987; Knight and Skagen 1988; Stalmaster and Kaiser 1997; Restani et al. 2000). Most such events in the Pacific Northwest occur during the non-breeding season (August-April), with breeding and non-breeding individuals dispersing throughout western North America (Servheen and English 1979; Stalmaster 1987; Buehler 2000). However, at Crescent Beach, British Columbia, we observed concentrations of up to 110 eagles feeding on spawning Plainfin Midshipman (*Porichthys notatus*) between March and June 1998-2002.

Although our observations were limited to Crescent Beach, midshipman may be an important prey item for breeding eagles at other locations in the Georgia Basin. For example, this species was the main food item delivered to young at nests near Crofton, eastern Vancouver Island (Gill and Elliott 2003). If this species is an important prey item, it could potentially be a significant vector for contaminants. Harfenist et al. (1995) sampled contaminant levels in 14 inshore fish species, and found the highest levels of some chlorinated hydrocarbon contaminants, including dioxins, in Plainfin Midshipman.

Methods and Study Area

We counted eagles along a 2.0 km stretch of waterfront around Crescent Beach, British Columbia, monthly from 1995 to 2002 (Figure 1). We used a 30× telescope at stations separated by about 200 m and situated on a railroad adjacent to and about 4 m above the shoreline. The survey extended from Crescent Beach (49°03.3N, 12°53.3W) south to 1001 Steps (49°02.0N, 123°52.5W).

To evaluate the importance of midshipman as a prey source for eagles, we observed 370 individual eagles for 10-minute intervals over 8-hour periods designed to cover all tide levels and times of day on nine days in May and June 2001. We used a 30× telescope positioned on the railroad adjacent to the shoreline at the location closest to the study subject. We noted the age (classified using Clark 2001) of each eagle, the identity and size relative to the eagle's bill length of all prey consumed, and whether any kleptoparasitism occurred. We also counted the number of eagles present every two hours.

Results and Discussion.

The two highest counts were 150 eagles in March 2001 (S. Boyd, personal communication) and 110 eagles on June 20, 1999 (KHE). The June count is the largest reported summer eagle concentration in southern British Columbia (Campbell et al. 1990).

During 90 hours of observation in May-June 2001 and 2002, the Plainfin Midshipman was the only prey item we observed eagles consuming at this location. This is a demersal fish that spawns in British Columbia's intertidal and high subtidal between May and July (Hart 1973; Elliott 2002). Most females and Type I

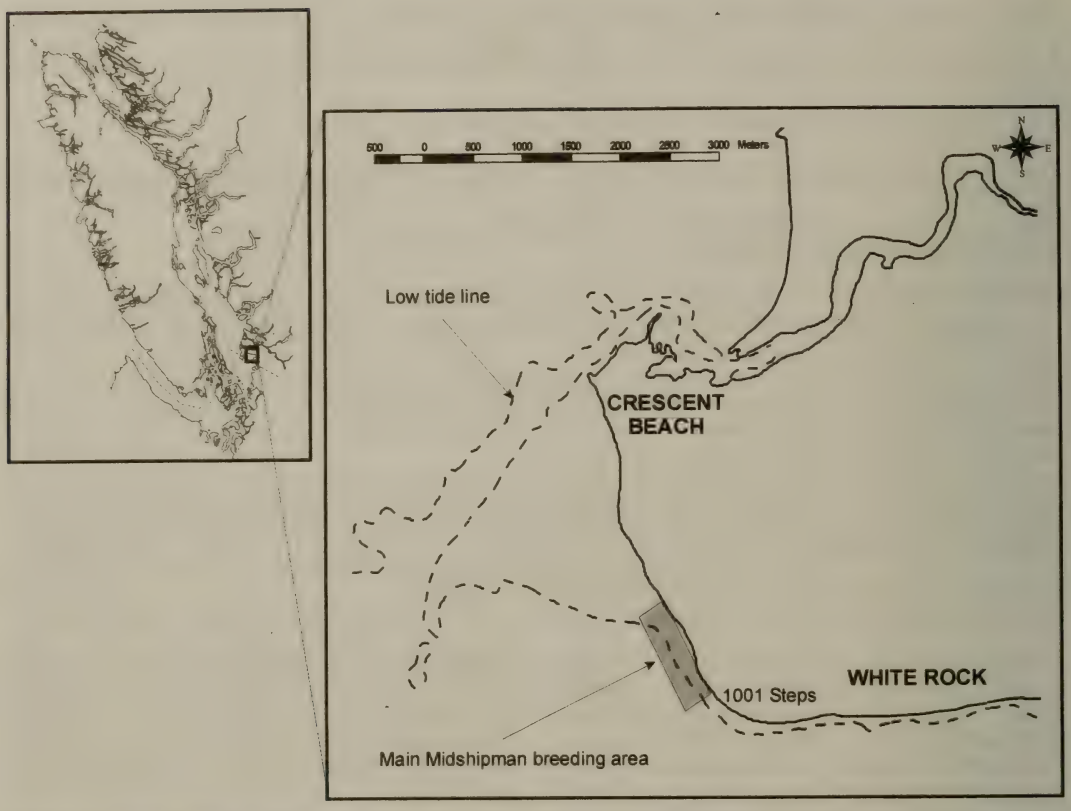


FIGURE 1. Location where Bald Eagles were observed to congregate and feed on Plainfin Midshipman, *Porichthys notatus*, from 1995 to 2002 near Crescent Beach, British Columbia.

(egg-guarding) males die after breeding (Demartini 1990; Elliott 2002). In addition to capturing emaciated post-breeders, the eagles also caught midshipman that were exposed on the beach or in shallow water by the receding tide, prior to breeding.

Between the first week in May and the last week in June, over 40 eagles (mean ± SE = 48.3 ± 1.3, n = 22) were consistently present at low tide (below 1.5 m). Eagles were not present along the foreshore at tides higher than 3 m, although some eagles were usually present in adjacent trees. Between 0.5 and 3 m, eagle counts decreased as tide height increased (Figure 2), with no difference between outgoing and incoming tides (ANCOVA, $P > 0.6$). Eagle counts did not vary with temperature, precipitation, time of day, or Julian date (correlation, $P > 0.6$). The overall ratio of subadults to adults was 1.19 to 1 and the proportions of subadults in each age class were 0.33 (1st years), 0.44 (2nd years), 0.15 (3rd years) and 0.08 (4th years). There was no difference in the timing of adult and juvenile counts (ANCOVA, $P > 0.6$).

The consumption rate also decreased at higher tide levels although consumption peaked between 1 and 2 m during outgoing tides, with no consumption occurring above 3 m (Figure 2). The overall consumption rate during outgoing tides was significantly higher than incoming tides only between 1 and 2 m (ANOVA, $F = 7.0$, $P = 0.03$). Consumption rate did not vary with temperature, precipitation, time of day, Julian date (correlation, $P > 0.6$) or individual's age (χ^2, $P > 0.6$). As predicted by Restani et al. (2000), we observed a significantly higher handling time by subadults (mean ± SE = 4.3 ± 0.8 min, n = 24) than adults (2.3 ± 0.4 min, n = 27). Handling time was independent of fish size (correlation, $P > 0.6$). Of fish consumed, 21% were pirated from conspecifics while 7% were pirated from Northwestern Crows (*Corvus caurinus*). There was no significant difference between adults and subadults in the proportion of fish pirated or the success of either age group at pirating one another (χ^2, $P > 0.6$). Overall, piracy was less successful (32% of all attempts successful, n = 62) than capturing prey (91% successful, n = 85).

Clearly, tide is the dominant environmental factor influencing the consumption rate and number of eagles at this location, as is also the case in the Columbia River estuary (Watson et al. 1991). The high consumption rate between 1-2 m on outgoing tides reflects

the consumption of midshipman exposed by the receding tide; most midshipman nest under boulders at the 1-2 m tide line. Assuming the consumption rates shown in Figure 2, an analysis of tide heights between sunrise and sunset from 10 May to 20 June in 2001 suggested that the average number of midshipman consumed per day per eagle was 14.2 ± 2.1, well above the amount needed for a neutral energy budget (Stalmaster and Gessaman 1984). This may explain why the eagles choose to conserve energy by loafing along the foreshore at low tide. We estimate that eagles consumed 22700 ± 3400 midshipman between 10 May and 20 June 2001, using the eagle counts from Figure 2. This would represent a large amount of nitrogen being transferred into nearby roost trees and may enhance community productivity along the shoreline, as has been observed near salmon spawns (Cederholm et al. 2000). The handling time for midshipman was shorter than that reported for Kokanee Salmon (*Oncorhynchus nerka*), where there was no difference in handling time between adults and juveniles (Restani et al. 2000). Although Bennetts and McClelland (1997) and Brown (1993) found lower foraging efficiencies in subadults than adults and Restani et al. (2000) found higher consumption rates in subadults, we found no difference in consumption rates, suggesting that experience plays a minor role in this system. Likewise, although the use of piracy decreases with age among eagles feeding on salmon (Bennetts and McClelland 1997), we found no difference in use of piracy between age classes. Hansen (1986) and Knight and Skagen (1988) showed that the success of eagles foraging on spawning salmon depends on the frequency of various strategies utilized at spawning sites. A similar analysis for eagles foraging on midshipman may elucidate some of the patterns described by other researchers that we were unable to find in our system, such as a relationship between age and consumption rates.

Eagle numbers in the Pacific Northwest have increased since the 1970s (Dunwiddie and Kuntz 2001; www.ecoinfo.org/env_ind/region/baldeagle/eagle_e.cfm [Buehler 2000]) and increased eagle predation may be contribute to low Great Blue Heron (*Ardea herodias*) reproductive success at some colonies (Vennesland

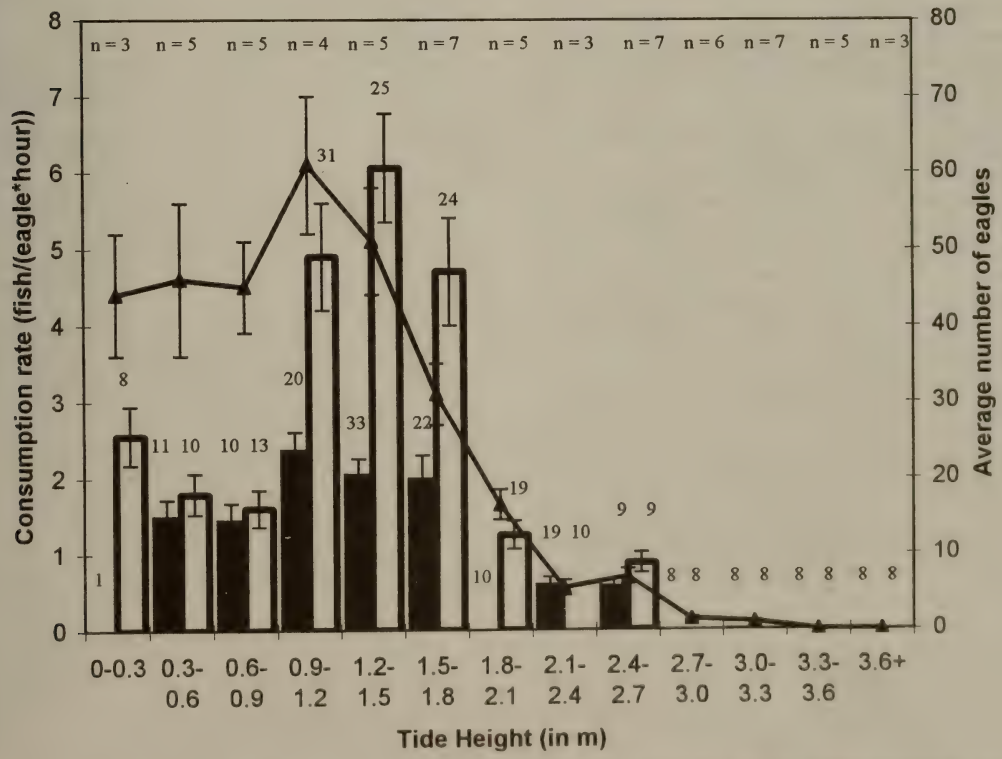


FIGURE 2. Consumption rate (black column = outgoing tide; white column = incoming tide) and average number of eagles on waterfront (line) as a function of tide height, at Crescent Beach, British Columbia, 1995–2002. Correlations on the unpooled data (tide height measured to the closest 10 cm) for all parameters are significant $P < 0.05$ (incoming consumption rate $r^2 = 0.66$, outgoing consumption rate $r^2 = 0.37$, average number of eagles $r^2 = 0.80$). Sample size shown above columns for consumption rates, top sample sizes are for counts. Error bars are ± SE.

2000). Anecdotal evidence from naturalists familiar with the area suggests that while midshipman have bred at Crescent Beach since at least the 1960s (J. D. Macphail, personal communication), large numbers of eagles were not observed until the mid-1990s (F. Cooke, personal communication). It is unclear if the increase in eagle predation has affected midshipman reproductive success, or if the eagles are replacing or competing with other predators; Northwestern crows, Glaucous-winged Gulls (*Larus glaucescens*) and Great Blue Herons also congregate to feed on spawning midshipman at Crescent Beach.

Acknowledgments

We would like to thank Fred Cooke for organizing the original waterbird surveys along Crescent Beach and J. Don Macphail for the original identification and basic natural history of the Plainfin Midshipman. Eric Taylor also provided information on the natural history of this species. Gary Bortolotti, and S. Lee created the map in Figure 1. A. J. Erskine and Rob Butler provided helpful comments on earlier drafts of this manuscript. In addition, we thank Clare Struik and Laura Jordison for their enthusiastic help in the field.

Literature Cited

Bennetts, R. E., and **B. R. McClelland.** 1997. Influence of age and prey availability on Bald Eagle foraging behavior at Glacier National Park, Montana. Wilson Bulletin 109: 393-409.

Brown, B. T. 1993. Winter foraging ecology of Bald Eagles in Arizona. Condor 95: 132-138.

Buehler, D. A. 2000. Bald Eagle (*Haliacetus leucocephalus) In* The Birds of North America (506). *Edited by* A. Poule and F. Gill. The Birds of North America, Inc., Philadelphia, Pennsylvania.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, and **M. C. E. McNall.** 1990. The birds of British Columbia. Volume 2: diurnal birds of prey through woodpeckers. Royal British Columbia Museum, Victoria, British Columbia.

Cederholm, C. J., D. H. Johnson, R. E. Bilby, L. G. Dominguez, A. M. Garrett, W. H. Graeber, E. L. Greda, M. D. Kunze, B. G. Marcot, J. F. Palmisano, R. W. Plotnikoff, W. G. Pearcy, C. A. Simenstad, and **P. C. Trotter.** 2000. Pacific salmon and wildlife – Ecological contexts, relationships, and implications for management. Special Edition Technical Report. Washington Department of Fish and Wildlife, Olympia, Washington.

Clark, W. S. 2001. Aging Bald Eagles. Birding 55: 120-124.

Demartini, E. E. 1990. Annual variation in fecundity, egg size and condition of the plainfin midshipman (*Porichthys notatus*). Copeia 1990: 850-853.

Dunwiddie, P. W., and **R. C. Kuntz II.** 2001. Long term trends of Bald Eagles in winter on the Skagit River, Washington. Journal of Wildlife Management 65: 290-299.

Elliott, K. H. 2002. Singing Fish. Vancouver Natural History Society. Discovery 31: 29-33.

Gill, C. E., and **J. E. Elliott.** 2003. The influence of contaminants and food supply on breeding success of Bald Eagles. Ecotoxicology 12: 95-112.

Hansen, A. J. 1986. Fighting behavior in Bald Eagles: A test of game theory. Ecology 67: 787-797.

Harfenist, A., P. E. Whitehead, W. J. Cretney, and **J. E. Elliott.** 1995. Food chain sources of polychlorinated dioxins and furans to Great Blue Herons (*Ardea herodias*) foraging in the Fraser River Estuary, British Columbia. Technical Support Series (169). Canadian Wildlife Service, Pacific and Yukon Region, Vancouver, British Columbia.

Hart, J. L. 1973. Pacific fishes of Canada. Bulletin of the Fisheries Research Board of Canada, Ottawa, Ontario.

Knight, R. L., and **S. K. Skagen.** 1988. Agonistic asymmetries and the foraging ecology of Bald Eagles. Ecology 69: 1188-1194.

Restani, M., A. R. Harmata, and **E. M. Madden.** 2000. Numerical and functional responses of migrant Bald Eagles exploiting a seasonally concentrated food source. Condor 102: 561-568.

Servheen, C., and **W. English.** 1979. Movements of rehabilitated Bald Eagles and proposed seasonal movement patterns of Bald Eagles in the Pacific Northwest. Raptor Research 13: 79-88.

Stalmaster, M. V. 1987. The bald eagle. Universe Books, New York, USA.

Stalmaster, M. V., and **J. A. Gessaman.** 1984. Ecological energetics and foraging behavior of overwintering Bald Eagles. Ecological Monographs 54: 407-428.

Stalmaster, M. V., and **J. L. Kaiser.** 1997. Winter ecology of Bald Eagles in the Nisqually River Drainage, Washington. Northwest Science 71: 214-233.

Vennesland, R. G. 2000. The effects of disturbance from humans and predators on the breeding decisions and productivity of the Great Blue Heron in south-coastal British Columbia. M.Sc. Thesis. Simon Fraser University, Burnaby, British Columbia.

Watson, J. W., M. G. Garrett, and **R. G. Anthony.** 1991. Foraging ecology of Bald Eagles in the Columbia River estuary. Journal of Wildlife Management 55: 492-499.

Received 11 October 2002
Accepted 12 January 2004

Do Female Northern Pintails, *Anas acuta*, Initiate Rapid Follicular Growth During Spring Migration?

PASCALE DOMBROWSKI[1], JEAN-CLAUDE BOURGEOIS[1], RICHARD COUTURE[2], and CHRISTIAN LINARD[3]

[1] Département de Chimie-Biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières, Québec G9A 5H7 Canada, and Société de la faune et des parcs du Québec, Direction de l'aménagement de la faune, 5575, Saint-Joseph, Trois-Rivières-Ouest, Québec G8Z 4L7 Canada
[2] Département de Chimie-Biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières, Québec G9A 5H7 Canada
[3] Département de Chiropratique, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières, Québec G9A 5H7 Canada

Dombrowski, Pascale, Jean-Claude Bourgeois, Richard Couture, and Christian Linard. 000. Do female Northern Pintails, *Anas acuta*, initiate rapid follicular growth during spring migration? Canadian Field-Naturalist 117(4): 605-610.

We describe the reproductive status of female Northern Pintails (*Anas acuta*) staging on a flooded plain along the St. Lawrence River (Quebec, Canada) during the spring of 1997. Nine of the 27 female pintails we collected had ovarian follicles showing Rapid Follicular Growth (RFG). In RFG females, total blood calcium and ash mass increased with follicular development. They had greater muscle and bone mass, and higher blood calcium levels, compared to pre-RFG birds. However, carcass fat mass and sex hormone levels (estradiol and progesterone) did not differ between the two groups. Our results indicate that at least some Northern Pintails initiate egg formation processes prior to arrival at nesting areas, which is consistent with early nesting. The nutrients and energy required for this early egg formation must come from reserves stored during winter, foods consumed in staging areas, or both.

Key Words: Northern Pintail, *Anas acuta*, staging, reproduction, ovarian follicle, growth, Quebec.

Northern Pintails (*Anas acuta*, hereafter called pintails) migrate and nest early (Fredrickson and Heitmeyer 1991; Austin and Miller 1995), and reach staging areas late March to early April (Austin and Miller 1995). Nesting season begins with ovarian follicle maturation in females, which must occur prior to egg laying. During Rapid Follicular Growth (RFG) and until ovulation, the ovarian follicles that will become eggs enlarge to form yolk from deposition of several lipid layers (Alisauskas and Ankney 1992; Joyner 1994). The diameter of the largest follicle distinguishes pre-RFG and RFG female ducks. In pintails, RFG begins when the diameter of this follicle reaches 8.2 mm and rapidly increases to 32.9 mm over about 4.2 days (Esler 1994). Serum sex hormone levels or blood concentration of calcium, phosphorus, and lipids, all of which increase during reproduction, might also be indirect indicators of reproductive status (Hannon 1979; Johnson 1986).

In female pintails, endogenous energy reserves for egg laying and incubation are important because incubating ducks may feed infrequently in contrast other nesting dabbling ducks generally do feed during incubation (Derrickson 1978; Ankney et al. 1991; Mann and Sedinger 1993). The accumulation of nutrient reserves (lipids, proteins, and calcium) to support reproduction thus occurs before egg laying (Mann and Sedinger 1993; Esler and Grand 1994). The only available information on pintail body composition relative to reproductive status is based on breeding females nesting in North Dakota (Krapu 1974) and Alaska (Mann and Sedinger 1993; Esler and Grand 1994; Flint and Grand 1996). Little is known about nutrient reserves and reproductive status of female pintails during spring migration.

In this study, we tested the hypothesis that female pintails prepare for egg laying during spring migration, a trait consistent with early nesting. First, we quantified the nutrient reserves and categorized reproductive status of collected female pintails on a spring staging site in the Lake St. Pierre region, Quebec. Second, we evaluated some of the physiological changes (ovary development and hormones) in the females during the pre-laying period. Finally, we examined the changes in different body components involved in reproduction.

Study Area and Methods

Sampling and specimen gathering

The study took place from 14 April to 9 May 1997 at the St. Barthelemy staging ground, located in the province of Quebec, Canada (46° 11' N, 73° 08' W). This staging site is in the Lake St. Pierre region, a Ramsar wetland site as well as a UNESCO Biosphere Reserve. Spring flood waters from the St. Lawrence River submerge this flood plain (5.0 to 6.0 m above sea level) for 5 to 6 weeks, beginning early April. The study site consists of 80 agricultural fields, for a total area of 246 ha. It is crossed by five drainage ditches and forms a deep basin. The staging area is managed to maintain water levels during spring waterfowl migration. The flooded fields of the study site are heavily used by pintails, which represent approximately 80% of the 10 000 dabbling ducks found in the area during 4 to 5 weeks. It is the second most important spring staging ground along the St. Lawrence River for dabbling ducks.

We used a .22 rifle to collect 27 female pintails. We weighed pintails (± 0.5 g) and took blood samples by intra-cardiac puncture (Donham 1979; Hannon 1979) into glass tubes (Vacutainer®, Becton-Dickinson, Rutherford, New Jersey, 07070 USA). We retained all samples on ice and in the dark until their arrival at the laboratory. At the lab, we centrifuged the blood samples, drew off the serum, and froze it at -20°C pending analysis.

We removed the ovarian follicles, esophagus, and gizzard from each carcass, and set the esophagi and gizzards aside pending food habits analysis. We measured the diameter (∅) of the largest follicle of each female with a calliper (±0.1 mm), and obtained follicular mass with a portable electronic balance (±0.1 g). We did not age the hens since both male and female pintails can breed at 1 year of age (Austin and Miller 1995). We divided the pintails into pre-RFG ducks, in which the diameter of the largest follicle was < 8.2 mm, and RFG ducks, in which diameters were ≥ 8.2 mm (Esler 1994). We stored carcasses at -30°C in sealed plastic bags.

Specimen analysis

We shaved frozen carcasses, then weighed them again (carcass weight), and cut them into pieces. We then ground the pieces twice in a meat grinder (Hobart®) to homogenize the components. We dried a 100-g sample of the homogenate to constant mass in a forced-air oven (60°C). We estimated percentage water for the sample and multiplied this by the frozen mass to determine carcass water mass and dry carcass mass (frozen mass – water mass). We ground the lyophilized sample in a high-speed grinder and took 1-g duplicates for lipid extraction (Gauthier et al. 1992). Carcass fat is percent fat in sample × dry carcass mass, hereafter called "fat".

We determined the mineral content of the carcass ("ash") by weighing the ash obtained by incinerating 2-3 g of lyophilized samples at 550°C for 12 hours. This value was then used to determine the ash weight of the dehydrated carcass. The protein content ("protein") was calculated using the following formula:

Protein mass = dehydrated carcass mass – (fat mass + ash mass) (Miller 1989; Dabbert et al. 1997).

Biochemical analyses

We considered many blood biochemical parameters which could indicate the reproductive status of female pintails. Previous studies showed that an increase in calcium can be observed in ovulating hens (Hochtleitner 1994), and a physiological hypercalcemia occurs in birds during egg laying (Amand 1986). Estrogen and progesterone are hormones involved in ovulation. Seasonal hypertrophy of the oviduct in free-ranging birds is dependent on estrogen, and progesterone interacts with estrogen in stimulating oviduct growth and secretory activity (Joyner 1994). On the basis of these studies and some preliminary work we did on specimens collected in the spring of 1996, we chose to quantify total calcium (Ca), estradiol (the main ovarian estrogen), and progesterone.

We used a Hitachi 704 automatic chemical analyzer (Boehringer Mannheim GmbH, Mannheim, Germany) to determine total calcium, with procedures and reagents supplied by the company (Gindler and King 1972). We measured estradiol and progesterone with a solid phase I^{125} radioimmunoassay using Coat-a-Count® kits (Diagnostic Products Corporation, Los Angeles, California, 90045-5597 USA), following the manufacturer's protocol. Because of the small size of serum samples available (1-2 mL), we did not analyze duplicates.

Statistical analyses

We tested all variables for normality, and even with transformed data, the conditions necessary for use of parametric tests were not met (i.e., normality was not achieved), so we used non-parametric tests. We used Spearman rank correlations (r_s) to analyze relationships among diameter of the largest follicle, total blood calcium, and ash mass (Bart and Notz 1994). We used the non-parametric Mann-Whitney comparison test to detect differences (between pre-RFG and RFG females) in body components, follicular mass, largest-follicle diameters, and blood biochemical parameters. We used SYSTAT™ for all analyses (White and Clark 1994), and we report all values as means +/- SE.

Results

Nine of the 27 female pintails we collected had ovarian follicles showing RFG (Figure 1). These 9 females had a mean follicle diameter of 12.0 ± 0.9 mm. Mean diameter for pre-RFG females was 5.7 ± 0.3 mm. The earliest date we collected RFG females was 21 April; none of the females collected between 14 and 20 April showed RFG, but all those collected after 2 May did (Figure 1a). For all females, diameter of the largest ovarian follicle increased as collection date advanced ($r_s = 0.71$, $P < 0.001$). Likewise, for RFG females ($n = 9$), total calcium levels ($r_s = 0.75$, $P < 0.05$, Figure 1b) and ash mass ($r_s = 0.85$, $P < 0.01$, Figure 1c) increased with increasing diameter of the largest follicle. Body mass (fresh and carcass), protein mass, ash mass, and total blood calcium of RFG females exceeded those of pre-RFG females (Mann-Whitney test, Table 1). However, carcass fat mass and sex hormone levels in the blood did not differ between pre-RFG and RFG groups (Table 1).

Discussion

Our results show that the pintails' staging period in St. Barthelemy coincides with the beginning of ovarian follicle maturation for some birds. At the end of the sampling period, all females we examined showed RFG, suggesting these female pintails were preparing for egg laying. This is consistent with the fact that

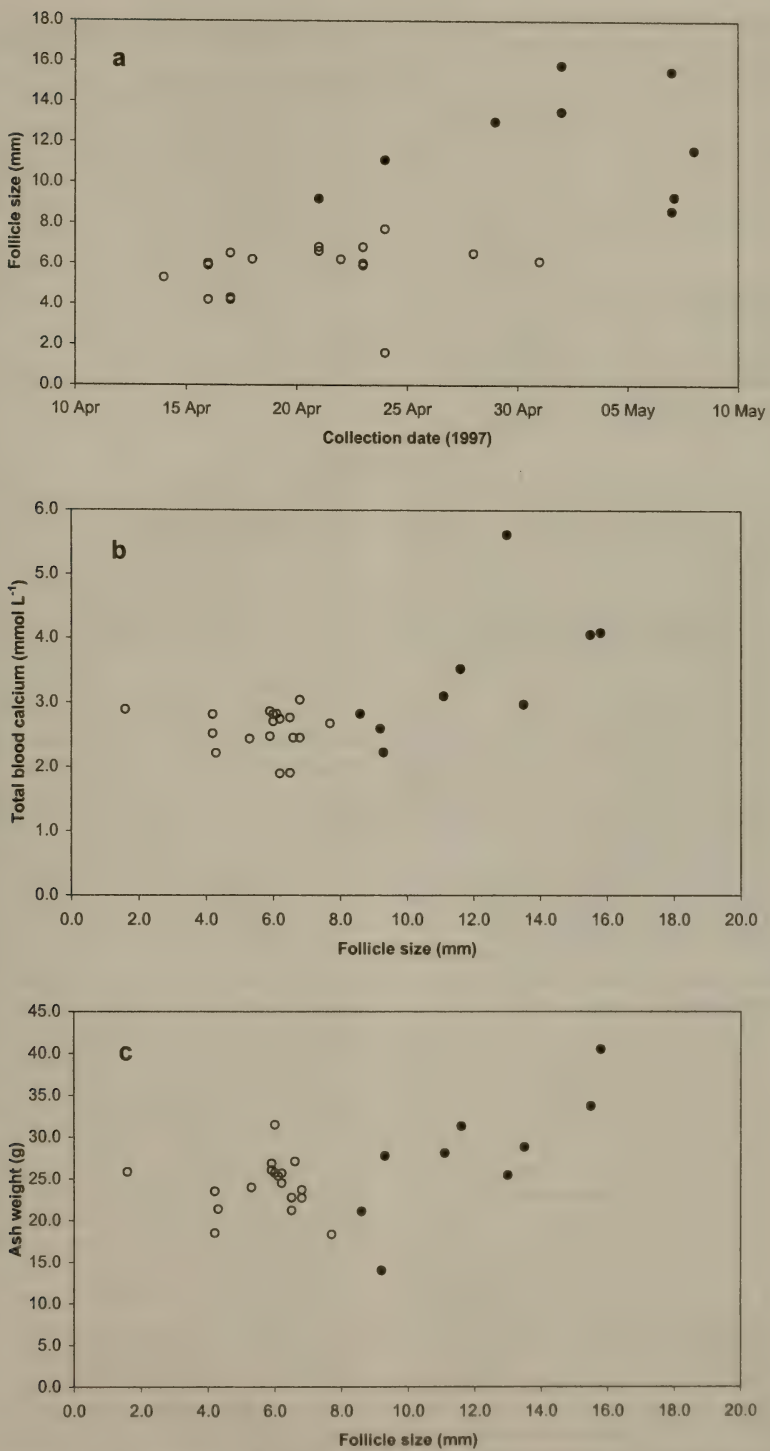


FIGURE 1. (A) Diameters of the largest ovarian follicle in the 27 female Northern Pintails sampled at staging ground in spring 1997 according to sample date. (B) Total blood calcium in the 27 female pintails sampled at staging ground in spring 1997 versus the largest ovarian follicle diameter. (C) Ash weight in the 27 female pintails sampled at staging ground in spring 1997 versus the largest ovarian follicle diameter. Solid circles represent the nine females in RFG stage (∅ > 8.2 mm, Esler 1994).

TABLE 1. Characteristics of pre-RFG and RFG female Northern Pintails (mean ± SE) during the spring migration stop of 1997. The last column gives the significance level when the two groups were compared using the Mann-Whitney test (ns: not significant, $P > 0.05$).

Characteristic	Pre-RFG ($n = 18$)	RFG ($n = 9$)	P
Carcass weight (g)	937.0 ± 16.8	1038.0 ± 25.2	< 0.01
Eviscerated weight (g)	825.5 ± 16.6	900.5 ± 22.3	< 0.05
Fat (g)	146.0 ± 9.6	168.5 ± 20.2	ns
Protein (g)	212.5 ± 14.2	258.0 ± 28.2	< 0.05
Ash (g)	24.0 ± 0.8	28.0 ± 2.5	< 0.05
Follicular mass (g)	1.3 ± 0.1	2.7 ± 0.4	< 0.001
Follicular diameter (mm)	5.7 ± 0.3	12.0 ± 0.9	< 0.001
Total calcium (mmol L^{-1})	2.6 ± 0.1	3.4 ± 0.3	< 0.01
Estradiol (pg mL^{-1})	52.4 ± 8.0 [a]	61.7 ± 15.1	ns
Progesterone (mmol L^{-1})	0.7 ± 0.2 [a]	0.6 ± 0.2	ns

[a] $n = 16$

pintails nest early (Austin and Miller 1995). No pre-RFG females were found after 2 May, which indicates that some females nest later, in more northern sites, and that they had already left. Because northern nesting sites are used at the end of May and early June, once the snow is melted, this might suggest that intermediary staging areas are used between these northern sites and St. Barthelemy.

The increase in blood calcium which accompanied increasing diameter of the largest follicles in RFG females suggested ducks obtained dietary calcium during ovarian follicle growth (Hohman 1986; Hochleitner 1994). The increased bone mass (ash) we found in females during RFG confirmed that calcium is stored in the medullary bones of female pintails. Medullary bone formation occurs during the reproductive period in some nesting female dabbling ducks (Johnson 1986; Kenny 1986), and is a source of calcium that can be rapidly mobilized during eggshell formation if dietary calcium is deficient (Sturkie 1986).

A difference in ash amounts between pre-RFG and RFG females has previously been reported for Wood Ducks (*Aix sponsa*) (Drobney 1982), Lesser Snow Geese (*Chen caerulescens caerulescens*) (Ankney and MacInnes 1978), and Ring-necked Ducks (*Aythya collaris*) (Hohman 1986). Increases in ash amounts and total calcium related to the diameter of the largest follicle have been reported in female Canvasbacks (*Aythya valisineria*) in Manitoba (Barzen and Serie 1990), domestic female Mallards (Fairbrother et al. 1990), and now in pintails. On the other hand, Mann and Sedinger (1993) saw no variations in ash amounts between pre-RFG and RFG pintails in Alaska during the pre-laying period. This may be a phenomenon associated with spring staging areas, where ducks from several different wintering areas and headed to different nesting regions, converge to forage and prepare for nesting on different schedules.

Like calcium, the proteins required for reproduction in females can be obtained in part from carcass reserves, as shown for Lesser Snow Geese (Ankney and MacInnes 1978), Greater Snow Geese (*Chen caerulescens atlantica*) (Choinière and Gauthier 1995), Common Eiders (*Somateria mollissima*) (Milne 1976), Canvasbacks (Barzen and Serie 1990), Gadwalls (*Anas strepera*) (Ankney and Alisauskas 1991), and pintails in Alaska (Mann and Sedinger 1993). For example, endogenous proteins provided 21-62% of the proteins necessary for egg production in Alaska (Mann and Sedinger 1993). In our study, female pintails in RFG contained more protein than did pre-RFG females. This suggested that, like Canvasbacks (Barzen and Serie 1990) and Gadwalls (Ankney and Alisauskas 1991), follicular growth does not occur until females accumulate a certain amount of protein or markedly increase protein in the diet. Observed differences in body protein between pre-RFG and RFG pintails (as was observed for blood calcium and ash) might also relate to diversity in wintering origins, migration strategies, and ultimate destinations, all of which are unknown for any collected bird. Further investigations using radio telemetry or stable-isotope studies might provide some suggestions on this.

Alisauskas and Ankney (1992) suggested waterfowl store nutrients (lipids, proteins, and minerals) before laying if, on average, they are unable to meet the daily cost of converting exogenous nutrients to egg nutrients simultaneously with egg production. Lipids are most often stored to take advantage of their high energy content (Alisauskas and Ankney 1992). Our study revealed no difference in fat content between pre-RFG and RFG females. These results may indicate that females do not store or accumulate fat between the two reproductive stages. They may also indicate the sample size was small, considering it was taken from a heterogeneous population on different reproductive schedules and strategies.

In female pintails from our study, progesterone and estradiol did not differ between pre-RFG and RFG stages. It only takes one bird in a small sample (9) to

cause statistical problems, but Donham's (1979) result regarding progesterone in female Mallards agrees with ours. However, that author reported higher estrone and estradiol 17-ß levels during nesting period. This indicates that estrone may be more appropriate for monitoring the reproductive status in birds. For example, in the Eastern Wild Turkey (*Meleagris gallopavo silvestris*), estrone was observed to be the predominant plasma estrogen and exhibited greater fluctuations than estradiol during breeding season (Martin et al. 1981).

The physiological changes we documented in pintail reproductive organs show that the St. Barthelemy staging site is used by females at various reproductive stages. Some females in RFG at the study site could have nested nearby, and not continue migrating. Indeed, pintail commonly nest in the Lake St. Pierre floodplain (Bélanger and Couture 1989). Our study therefore suggests the nutrients and energy required for early egg formation must come from reserves stored during winter, foods consumed in staging areas, or both.

Acknowledgments

This study was made possible thanks to the financial support of La Fondation Héritage Faune (Fédération québécoise de la faune) and La Fondation de la faune du Québec, and grants from La Fondation Universitaire du Centre du Québec and l'Université du Québec à Trois-Rivières (UQTR). We thank the staff of La Société de la faune et des parcs du Québec for their technical support and Gilles Gauthier (Université Laval) for allowing us to use his equipment for carcass analysis. We appreciated the helpful comments of Antoine Aubin (UQTR), Hélène Glémet (UQTR), and Gilles Gauthier. We also thank Laure Devine and Brigitte Duval for reviewing this manuscript.

Literature Cited

Alisauskas, R. T., and **C. D. Ankney.** 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pages 30-61 *in* Ecology and management of breeding waterfowl. *Edited by* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu. University of Minnesota Press, Minneapolis, Minnesota.

Amand, W. B. 1986. Avian clinical hematology and blood chemistry. Pages 264-276 *in* Zoo and wild animal medicine, 2nd edition. *Edited by* M. E. Fowler. W. B. Saunders, Philadelphia, Pennsylvania.

Ankney, C. D., and **R. T. Alisauskas.** 1991. Nutrient-reserve dynamics and diet of breeding female gadwalls. Condor 93: 799–810.

Ankney, C. D., and **C. D. MacInnes.** 1978. Nutrient reserves and reproductive performance of female lesser snow geese. Auk 95: 459–471.

Ankney, C. D., A. D. Afton, and **R. T. Alisauskas.** 1991. The role of nutrient reserves in limiting waterfowl reproduction. Condor 93: 1029–1032.

Austin, J. E., and **M. R. Miller.** 1995. Northern Pintail (*Anas acuta*). *In* The birds of North America, number 163. *Edited by* A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.

Bart, J., and **W. Notz.** 1994. Analysis of data. Pages 24–74 *in* Research and management techniques for wildlife and habitats, 5th edition. *Edited by* T. A. Bookhout. The Wildlife Society, Bethesda.

Barzen, J. A., and **J. R. Serie.** 1990. Nutrient reserve dynamics of breeding canvasbacks. Auk 107: 75–85.

Bélanger, L., and **R. Couture.** 1989. Pintail, *Anas acuta*, use of man-made ponds in Quebec. Canadian Field-Naturalist 103: 547–550.

Choinière, L., and **G. Gauthier.** 1995. Energetics of reproduction in female and male greater snow geese. Oecologia 103: 379–389.

Dabbert, C. B., T. E. Martin, and **K. C. Powell.** 1997. Use of body measurements and serum metabolites to estimate the nutritional status of mallards wintering in the Mississippi Alluvial Valley, USA. Journal of Wildlife Disease 33: 57–63.

Derrickson, S. R. 1978. The mobility of breeding Pintails. Auk 95: 104–114.

Donham, R. S. 1979. Annual cycle of plasma luteinizing hormone and sex hormones in male and female Mallards (*Anas platyrhynchos*). Biology of Reproduction 21: 1273–1285.

Drobney, R. D. 1982. Body weight and composition changes and adaptations for breeding in wood ducks. Condor 84: 300–305.

Esler, D. 1994. Dynamics of ovarian follicles in breeding ducks. Wilson Bulletin 106: 679–688.

Esler, D., and **J. B. Grand.** 1994. The role of nutrient reserves for clutch formation by Northern Pintails in Alaska. Condor 96: 422–432.

Fairbrother, A., M. A. Craig, K. Walker, and **D. O'Loughlin.** 1990. Changes in mallard (*Anas platyrhynchos*) serum chemistry due to age, sex, and reproductive condition. Journal of Wildlife Disease 26: 66–77.

Flint, P. L., and **J. B. Grand.** 1996. Variation in egg size of the Northern Pintail. Condor 98: 162–165.

Fredrickson, L. H., and **E. Heitmeyer.** 1991. Life history strategies and habitat needs of the northern pintail. U. S. Fish and Wildlife Service, Fish and Wildlife Leaflet number 13.1.3, 8 p.

Gauthier, G., J.-F. Giroux, and **J. Bédard.** 1992. Dynamics of fat and protein reserves during winter and spring migration in greater snow geese. Canadian Journal of Zoology 70: 2077–2087.

Gindler, E. M., and **J. D. King.** 1972. Rapid colorimetric determination of calcium in biological fluids with methylthymol blue. American Journal of Clinical Pathology 58: 376–382.

Hannon, S. J. 1979. Plasma calcium as an indicator of reproductive condition in female blue grouse. Journal of Wildlife Management 57: 463–465.

Hochleitner, M. 1994. Biochemistries. Pages 223–245 *in* Avian medicine: principles and application. *Edited by* B. W. Ritchie, G. J. Harrison, and L. R. Harrison. Wingers Publishing, Lake Worth.

Hohman, W. L. 1986. Changes in body weight and body composition of breeding ring-necked ducks (*Aythya collaris*). Auk 103: 181–188.

Johnson, A. L. 1986. Reproduction in the female. Pages 403–431 *in* Avian physiology, 4th edition. *Edited by* P. D. Sturkie. Springer-Verlag, New York.

Joyner, K. L. 1994. Theriogenology. Pages 748–804 *in* Avian medicine: principles and application. *Edited by* B. W. Ritchie, G. J. Harrison, and L. R. Harrison. Wingers Publishing, Lake Worth.

Kenny, A. D. 1986. Parathyroid and ultimobranchial glands. Pages 466–478 *in* Avian physiology, 4th edition. *Edited by* P. D. Sturkie. Springer-Verlag, New York.

Krapu, G. L. 1974. Feeding ecology of Pintail hens during reproduction. Auk 91: 278–290.

Mann, F. E., and **J. S. Sedinger.** 1993. Nutrient-reserve dynamics and control of clutch size in Northern Pintails breeding in Alaska. Auk 110: 264–278.

Martin, R. M., M. E. Lisano, and **J. E. Kennamer.** 1981. Plasma estrogens, total protein, and cholesterol in the female eastern wild turkey. Journal of Wildlife Management 45: 798–802.

Miller, M. R. 1989. Estimating carcass fat and protein in Northern Pintails during the nonbreeding season. Journal of Wildlife Management 53: 123–129.

Milne, H. 1976. Body weights and carcass composition of the common eider. Wildfowl 27: 115–122.

Sturkie, P. D. 1986. Avian physiology. Fourth edition. Springer-Verlag, New York, New York.

White, G. C., and **W. R. Clark.** 1994. Microcomputer applications in wildlife management and research. Pages 75–93 *in* Research and management techniques for wildlife and habitats, 5th edition. *Edited by* T. A. Bookhout. The Wildlife Society, Bethesda.

Received 4 December 2002
Accepted 15 April 2004

Supposed Periodicity of Redpoll, *Carduelis* sp., Winter Visitations in Atlantic Canada

ANTHONY J. ERSKINE[1] and REID MCMANUS, JR.[2]

[1]16 Richardson Street, Sackville, New Brunswick E4L 4H6 Canada
[2]657 Royal Road, Memramcook, New Brunswick E4K 1X1 Canada

Erskine, Anthony J., and Reid McManus, Jr. 2003. Supposed periodicity of Redpoll, *Carduelis* sp., visitations in Atlantic Canada. Canadian Field-Naturalist 117(4): 611-620.

Redpoll (primarily *Carduelis flammea*) data from the New Brunswick–Nova Scotia border region were reviewed in the context of alleged biennial periodicity of irruptions south of their breeding range. Long-term records by the authors suggested a number of departures from visitation in alternate years. Three local Christmas Bird Counts (CBCs) spanning the last 41 winters supported the less-than-regular pattern shown by individual observations. CBC redpoll data from across the Atlantic Provinces revealed annual redpoll visitations across southern New Brunswick, where the largest regional counts (adjusted for observer effort) usually occurred. Visitation to Prince Edward Island, Nova Scotia, and Newfoundland was less frequent, and patterns there were often obscured by scarcity of CBCs with both long-run coverage and redpolls. Examination of those data in relation to varying food availability suggested that irregular abundance but near-annual occurrence of redpoll visitation explains observed observations better than attempts to find periodicity in their irruptions.

Key Words: Common Redpoll, *Carduelis flammea*, Atlantic Provinces, winter, irruptions, periodicity, food availability.

Redpolls (here discussed as *Carduelis flammea; C. hornemanni* is rare – and under-detected – in our region) breed in the subarctic all around the northern hemisphere. Their occurrence south of the breeding range varies between years and areas, some northern-wintering areas holding redpolls in most years, whereas more southern areas have them less frequently.

Several publications discussed "biennial periodicity" in Common Redpoll movements to their winter ranges, but seldom defined unambiguously what they meant by periodicity. The most usual pattern featured southward irruptions mainly or entirely in winters starting in odd-numbered years, but such movements varied greatly – in size and distribution – between areas and years. Given biological variation, that was to be expected, but one was left wondering what each author considered as periodicity.

Kennard (1976) used banding totals from 1955-1972, mostly in the northern USA in winter and early spring. Bock and Lepthien (1976) used Christmas Bird Counts (CBCs), in early winter, from 1962-1971, in USA and southern Canada, but included very few (if any) from Atlantic Canada. Troy (1983) examined banding recaptures (none mapped as to or from the Maritimes) for periodicity, distribution, and return to areas used earlier; Brewer et al. (2000) reviewed larger samples of band recoveries – but still none from the Maritimes – for distribution. Houston et al. (2000) cited banding data (1960-2000) and CBC data (1956-2000), in Saskatchewan and Manitoba, but focused on the (at Saskatoon) exceptionally large irruption of 1999-2000. Those data-sets were judged to support "biennial periodicity", to varying degrees.

Hochachka et al. (1999) reviewed earlier studies, noting limited geographic distribution of banding effort and limited seasonal sampling by CBCs. Hochachka et al. (1999) used data from Project FeederWatch, which partly avoided those limitations, but their paper (mainly using FeederWatch data for one winter, 1993-1994) did not address periodicity directly. They concluded that some redpoll movements occur every year, so these should be viewed as irruptive migration rather than nomadism. They acknowledged that "migration" in redpolls – unlike that of typical migrants – does not often link breeding areas to the same wintering areas each year.

Larson and Bock (1986) examined redpoll CBC data over a longer period (1901-1980), and concluded that "the pattern and synchrony of (redpoll) eruptions… can decay and reform over long periods of time and that such patterns were especially weak between 1921 and 1950…". Their graphs also showed some departures from a biennial pattern in earlier and later time periods.

Variations in distance and numbers in redpoll movements generally are assumed to be food-driven. Evidence of this is circumstantial, and we have no new data on it. Southward movements presumably are triggered by food shortage in breeding areas, and continue until food – in the east, especially seeds of birches or alders (Betulaceae) – is found in sufficient quantity to attract transient flocks (Newton 1972), which often are large. Large seed crops of those tree/shrub species, in breeding and northern wintering areas, occur more or less biennially (some references given by Kennard 1976, and Bock and Lepthien 1976), but northern data are scanty where human populations are sparse and economic importance of those trees is slight. Redpolls feed on those seeds (where present), but we know little about relations between levels of seed-crops of those trees and numbers of the birds. Until studies are

done on this, the role of food-sources in irruptions is only a working hypothesis.

Variations in geography produce many departures from strict latitudinal zonation. Temperature isotherms in summer dip steeply across Canada from northwest to southeast; redpolls breed in the subarctic zone of Alaska and Yukon at latitude 60-70°N (Godfrey 1986), but average 10° farther south from northern Ontario east to Labrador (Todd 1963; Cadman et al. 1987; Gauthier and Aubry 1996). Redpoll winter range in the prairie provinces follows the north edge of treeless prairies southeast from 54°N in Alberta to 50° in Manitoba (e.g., Smith 1996), fanning out into wooded areas farther southeast (e.g., Cyr et Larivée 1995). East of longitude 65°W much area between latitude 47° and 50°N is occupied by the Gulf of St. Lawrence and connecting bays and channels, offering no habitat for redpolls – which in Atlantic Canada must winter farther north or farther south.

Weather patterns also vary geographically. Owing to the convergence, east of 65°W, of west–east and southwest–northeast storm tracks (Bryson 1966), weather in Atlantic Canada is more unsettled at all seasons than farther west (AJE, personal observation). That probably influences year-to-year variation in habitat suitability for redpolls. Thus, redpoll occurrence patterns likely differ between Atlantic Canada and more western parts of their range in North America.

Our field data on redpolls in southeast New Brunswick and adjacent Nova Scotia, together, spanned longer time-periods than databases used in other studies cited (except Larson and Bock 1986), in a region from which few or no data were available to earlier workers. Our observations were supplemented by data from many CBCs in the Atlantic Provinces, to explore occurrence or absence of patterns over time.

Data sources and methods

Our field data-sets were based on opportunistic, thus frequently irregular, coverage. McManus (McM) has lived all his life in Memramcook, New Brunswick (46°00'N, 64°33'W), where he studied birds since 1928. McM noted every bird he saw some winters, but his notes are missing for some other winters; worktime commitments often limited his opportunities for observing and recording data. Before 1940, he seemingly did not recognize redpolls by their calls, so his field notes provided information on incursions mainly in 1940–74. Gaps in his observations or note-keeping sometimes obscured local status of redpolls in the 1940s and 1950s.

Erskine (AJE) lived in Sackville, New Brunswick (45°54'N, 64°22'W), in 1960-1968 and 1977–present. His local field activity extended across the Chignecto Isthmus region (area ca. 60 × 40 km, in MS in prep.). AJE noted redpolls whenever encountered in winter, but he worked elsewhere in parts of some winters. Gaps in AJE records resulting from absences from the area were easily distinguished from times when no redpolls were seen.

Three local CBCs, near Sackville and Cape Tormentine, New Brunswick, and Amherst, Nova Scotia, all with annual coverage 1961–present, provided local comparisons. Selected CBCs elsewhere in New Brunswick, Nova Scotia, Prince Edward Island, Newfoundland – not including Labrador (see Figure 1 and Appendix 1 for CBCs used and locations) – extended the picture geographically. Only CBCs with near-annual coverage for ~20 years or more, and with redpolls reported in 10+ years, were used. Long-run counts that rarely or never reported redpolls were ignored, as were CBCs surveyed in <20 years. Most data were taken from regional publications – *N.B. Naturalist* (earlier *Nature News*), *Nova Scotia Birds* (earlier *N.S. Bird Society Newsletter*), *Island Naturalist* (Prince Edward Island), and *Osprey* (Newfoundland); Audubon compilations were much less complete for this region, and duplicated only parts of coverage published locally.

Because effort deployed on CBCs varied greatly (mostly increasing over the study period), all redpoll counts reported were adjusted (roughly) to "counts per 10 party-hours". This made direct comparisons easier between counts with many vs. few observers. The proportions of zero counts (absence, vs. presence, of redpolls) often seemed as informative as maximum (or modal) counts, as a few large counts were reported in years when most CBCs found no redpolls.

Geographic patterns in Atlantic Canada CBC redpoll data encouraged dividing that data-set, for some comparisons, among seven sub-regions (see Appendix 1 and Figure 1 for CBCs in each sub-region):

- N–NB: 6 CBC circles in New Brunswick north of latitude 46°40'N;
- S–NB: 10 circles in New Brunswick south of above, and north of latitude 45°20'N;
- ScoNB: 5 circles in New Brunswick south of above, and adjoining south (Bay of Fundy) coast;
- Bord: 3 circles in New Brunswick–Nova Scotia border area; these counts were discussed separately as "Local CBCs", but generally showed occurrence patterns similar to those in S–NB;
- N–NS/PE: 6 circles, 3 in Prince Edward Island, 3 in east Nova Scotia (including Cape Breton Island) north of latitude 45°15'N;
- S–NS: 7 circles in Nova Scotia south and west of above;
- INF: 7 circles in insular Newfoundland.

Results

Timing of redpoll visitations to New Brunswick – Nova Scotia border area

In years when redpolls visited our area, first detections ranged from September to December. McM found single redpolls 30 September 1971, 3 October 1947, and 5 October 1948; he noted no other arrivals

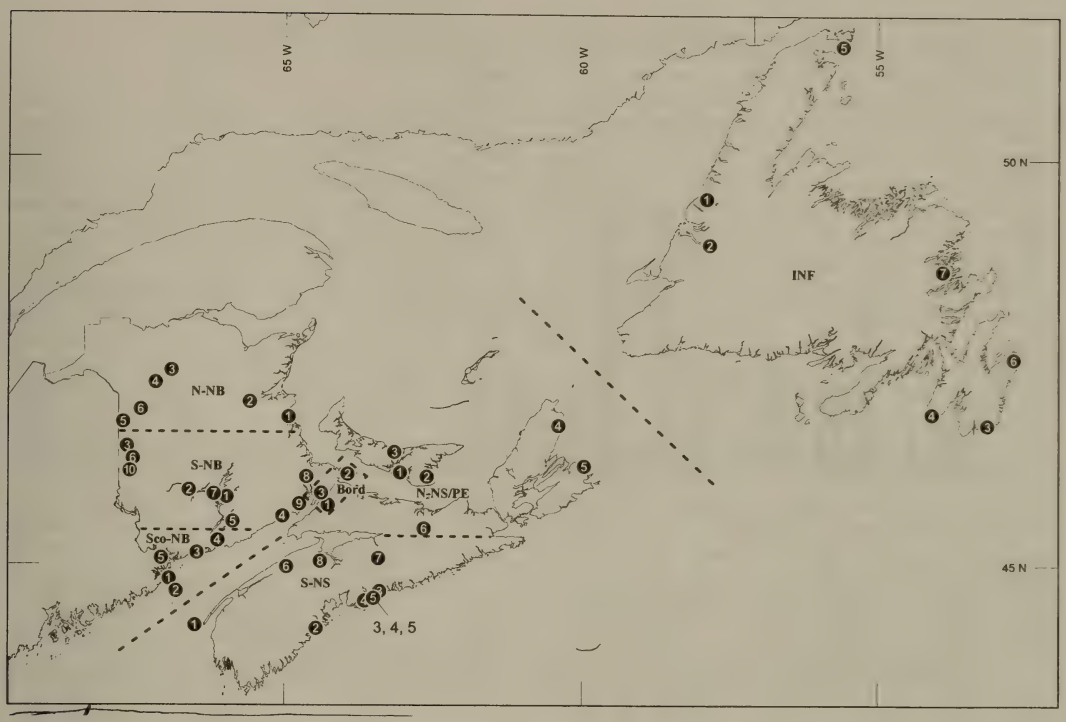


FIGURE 1. Christmas Bird Counts (CBCs) used in redpoll study in Atlantic Provinces, grouped by sub-regions (defined in text, see also Appendix 1). The numbers follow the sequence of entries in Appendix 1.

before mid-October, and AJE's earliest was 31 October 1965. Most arrivals were in November or December. In years when both saw them, McM detected redpoll arrivals earlier than AJE, through regular feeder-watching at home (AJE fed these birds only from 1995). Arrival dates seemed unrelated to size of a winter's redpoll incursion.

Redpolls were in our area, in different winters, for a few days to several months. When many redpolls visited, last sightings usually were in March or April, a few in early May, but large visitations sometimes ended by late February. Departure dates seemed unrelated to numbers or frequency of sightings in the area that year. In winters with few redpolls, records might be scattered through the season, or grouped in a single month; sparse records might reflect observation gaps as much as absence of redpolls.

Comparison of observers and areas

McM and AJE both observed, with varying regularity, in nearby areas of New Brunswick in winters of 1960-1961 thru 1967-1968 (plus March 1960 and November–December 1968); after AJE returned to Sackville in September 1977, McM kept few notes of redpolls. Our overlap in coverage here thus spanned eight full winters and parts of five more – of 72 winters when one or both was/were active here.

In the overlap periods, both noted some redpolls in 10 winters, and in two neither saw any. In 1962-1963 AJE saw one flock, and McM none. In the two winters when both found substantial redpoll numbers, AJE was in Sackville only briefly, arriving 18 March 1960, and leaving 10 December 1968; his few local notes in those winters suggested sizable numbers present.

Except for first arrivals, our detection of redpolls seemed generally comparable, and our data were treated as equivalent in other comparisons.

Local observations

Our data from the New Brunswick–Nova Scotia border region from 1940-1941 to 2001-2002 are summarized in Figure 2 (see also Appendix 2). Those data, based on often variable coverage, sometimes suggested large redpoll "flights" in alternate winters – as reported by observers elsewhere. However, departures from that pattern often were obvious. Sizable redpoll visitations were noted in successive winters [1948-1949 and 1949-1950; 1968-1969 and 1969-1970; 1986-1987 and 1987-1988], and sometimes two, three, or more winters intervened between sizable irruptions [1943-1944 to 1946-1947; 1949-1950 to 1952-1953; 1952-1953 to 1957-1958 (gaps); 1965-1966 to 1968-1969; 1973-1974 to 1980-1981 (gaps); 1983-1984 to 1986-1987; 1987-1988 to 1991-1992]. Some

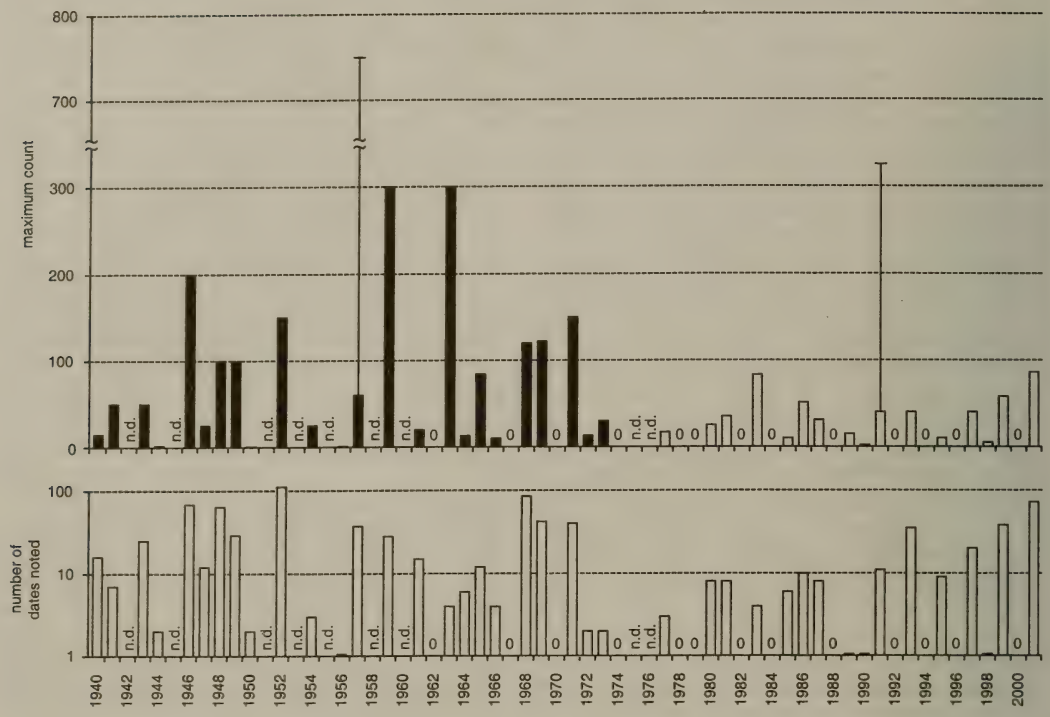


FIGURE 2. Maximum counts of redpolls (upper) and number of dates noted (lower, log scale), for each winter starting in year shown, observed by McManus near Memramcook (black), and by Erskine near Sackville (white), in New Brunswick. Extended lines show outliers, solid or open bar indicating the 2nd highest count in that year.

longer "runs" with few or no redpolls, especially 1952-1958 and 1973-1980, were influenced in part by irregular coverage; others likely were real.

Of those 62 winters, 53 with data, we noted no redpolls at all in only 13, thus detecting some redpolls in three-quarters of the winters. In 8 of those winters, our sightings totalled <10 redpolls each winter. If visitations were strictly "biennial", we might have expected 27 of 53 winters to have very few or no redpolls detected. Some small visitations likely were missed by our varying effort, so comparisons with other regional data may give better perspective on periodicity of redpoll incursions.

Local CBCs

The three local CBCs included a few observations (by McM and AJE) treated above, but such data comprised very minor proportions of those counts. CBCs involve larger numbers (seen by multiple observers), but their samples are restricted to one day in early winter each year; they may be biased if adverse conditions occurred on count day – or if birds were misidentified. "First arrivals" in December sometimes were on CBCs, in years when observation time was limited earlier in fall.

All three local CBCs were active in 41 winters (1961-2001), but effort on each count increased gradually from 2-5 observers at first to 15-20 from about 1980, with observer expertise improving as well. Only in 6 (of 41) winters were no redpolls reported on any of those CBCs, and in 6 other years redpolls (1–11/yr) were noted only on one count. Local CBCs usually matched personal observations as to scarcity or absence. As in our observations, these birds were found (in numbers >10) on CBCs in far more winters than might be expected if "biennial periodicity" was the major or only factor controlling redpoll occurrence.

If redpolls often moved into or through our area before or after the CBC period, season-long observations should have detected those birds in some years when none were met on CBCs, despite the larger observer effort in the latter exercise. Actually, the local CBCs detected redpolls in an even larger proportion of winters than McM and AJE did. A look at redpoll data from a wider geographic scene seemed desirable.

Other Atlantic Provinces CBCs

Within the Atlantic Provinces, CBC coverage (minimal before 1960) expanded steadily up to 1980, in numbers both of counts and of observers. In 1980-

2000, useful data (defined under "Data sources...") were available annually from 40–45 regional CBCs, combining reports of about 700 observers. Redpoll data from regional CBCs (1960-2000) showed variable visitation patterns when data were subdivided geographically. Figure 3 shows CBC data from New Brunswick only; see Appendix 3 for other areas and extra details.

One pattern that emerged from study of Figure 3 and Appendix 3 was the near-annual concentration of redpolls in southern N.B. inland from the Bay of Fundy (subregions S–NB and Bord). Redpolls were reported in S–NB, on some or all CBCs, in all 41 winters covered by the CBC data-set, and the highest single count (adjusted for effort) annually was in S–NB in fully half those years. Highest regional counts mostly were at one of six CBCs, all in S–NB or Bord, near latitude 46°N – Woodstock, Fredericton, Jemseg, Cambridge-Narrows, Moncton, Cape Tormentine. Concentration of redpolls occurred in southern New Brunswick whether the overall "flight" into (and through?) the Maritimes was large or small.

The (mostly) much smaller samples in N–NB showed less consistent patterns, but adjusted counts there in major flight years were generally lower than in S–NB. Counts still farther south (ScoNB, S–NS) also were usually lower than in S–NB. In years with small but widespread redpoll numbers elsewhere, often none were found in those two southern sub-regions.

The more eastern sub-regions (N–NS/PE, INF; Figure 3) were sparsely and often inconsistently sampled by CBCs. Few large (adjusted) counts occurred in INF even in major flight years (Appendix 3). In Prince Edward Island, maximum counts in 1997 and 1999 matched those in S–NB, but in most winters with many redpolls in New Brunswick numbers were much lower in Prince Edward Island; the few long-run counts in eastern Nova Scotia showed no consistent patterns.

A few high counts ("outliers") fell far outside the ranges on other CBCs in the same years. Such "outliers" may have represented "mass movements" in progress, or just after arrival and before dispersal. The 1991 Cape Tormentine CBC (unadjusted 14 159 birds, adjusted 3540) involved flocks moving all day ESE–WNW across the circle, thus from northern Nova Scotia into southern New Brunswick. Major incursions to N–NB and S–NB occurred in 1991, but elsewhere in the Maritimes only Glace Bay had an unusually large count (Appendix 3). Other obvious "outliers" at St Anthony (INF; 1976 – 3885 unadjusted) and Kouchibouguac National Park (N-NB; 1990 – 1233 unad-

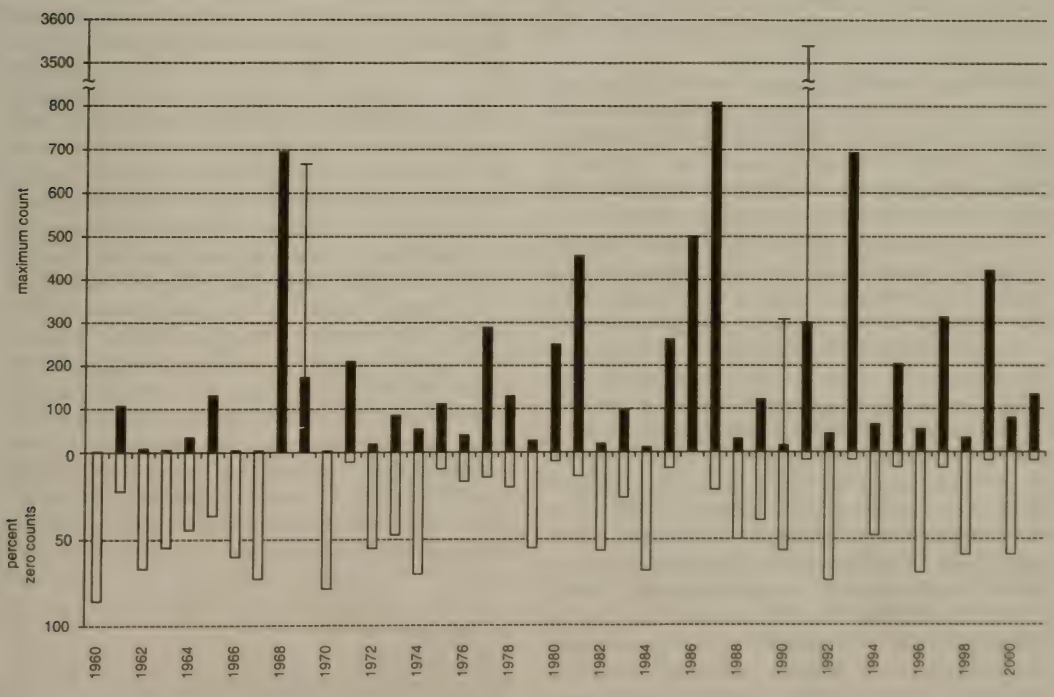


FIGURE 3. Adjusted maximum counts (above x–axis) and percent zero counts (below x–axis, vertical scales differ) of redpolls in New Brunswick CBCs during each winter starting in year shown. Extended lines indicate outliers (as above).

justed), were in years with minor visitations elsewhere. Outliers at Wolfville (S-NS; 1999 – 4511 unadjusted), St Andrews (ScoNB; 1969 – 800 unadjusted) and Brier Island (S-NS; 1964 – 200 unadjusted) were in areas where high (adjusted) counts always were unusual.

Discussion

What is left of "biennial periodicity" when many exceptions occur?

Periodicity involving "cycles" with several years between peaks and troughs may not be seriously obscured by irregularities in cycle-length (e.g., Keith 1963), but a short cycle has little space for exceptions. With a biennial rhythm, a "high" year when a "low" is expected produces either three "highs" in a row, or displaces the next "low" to three years after the previous one. Either way, periodicity is lost.

Our own observations (Figure 2) and the New Brunswick CBC data set (Figure 3) showed some periods of alternating winters with (variably) high vs. low or no redpolls, *separated by periods when redpoll occurrence did not fit that (or any?) pattern*, thus:

McM/AJE – high-low alternation in 1959-1960 to 1966-1967, 1969-1970 to 1973-1974, 1981-1982 to 1985-1986, 1989-1990 to 2001-2002;

NB CBCs – high-low alternation in 1969-1970 to 1977-1978, 1981-1982 to 1985-1986, 1987-1988 to 2001-2002. The three later periods of high-low alternation in CBC redpoll counts thus overlapped with similar periods in the McM/AJE data; the first period of alternation in McM/AJE data was not evident in the few CBCs made in S–NB then.

CBC data from Nova Scotia and Prince Edward Island (Appendix 3) also showed high-low alternation of redpoll numbers in 1988-89 to 2001-02, but not in earlier periods. Alternation was never obvious in CBCs from insular Newfoundland, where CBCs and large counts of redpolls were generally scarce.

All methods used here for assessing redpoll "flights" – as large vs. small/absent – are imperfect. Restriction of CBCs to a two-week span of dates makes those data vulnerable to bias, including adverse conditions on count days. With 20+ counts, scattered through the allowable periods, in most years from 1980, that bias seemed unlikely to be important in New Brunswick then, but it may have blurred earlier comparisons there, and all comparisons using the few (6–7) long-run counts in INF and N–NS/PE sub-regions. CBCs sample only early winter status, whereas redpoll movements often continue erratically through the winter. Despite often irregular coverage, McM/AJE surveys in most winters may have represented redpoll status as well as (or better than) the sparser sampling by CBCs before 1980. Regional data thus suggested that "biennial periodicity" in redpoll occurrence and numbers, if any, was frequently obscured by other factors. Redpoll irruptions to the Maritimes occur every year, as remarked more generally by Hochachka et al. (1999), but wide variation in numbers, timing, and distribution here indicates that these movements are not normal (annual) migrations.

Numerical variations in winter range arise from factors operating in redpoll breeding areas

Seed-set in birches, in relation to breeding success of redpolls, has not been studied in northern Canada, but any substantial failure of birch seed-crop in redpoll breeding areas presumably results in an exodus from there before the next winter. For survival of trees there, a missed seed-crop would be "made up" in the next summer, if possible; it would not be delayed another year merely to maintain a pattern of good seed-crops (when few redpolls move southward) only in alternate years. Further, adverse conditions in consecutive summers could result in successive failed seed-crops in a region, leading to major redpoll exodus in successive winters. However, trees "programmed" for a biennial seed-set cycle would not often be able, even under favourable conditions, to produce large seed-crops in successive years (allowing redpolls to remain there through the next winter). Successive years without sizable southward movements of redpolls thus would be less frequent than successive years with such exodus. CBC data suggested successive "lows" in New Brunswick in winters of 1962-1963 and 1963-1964, and 1966-1967 and 1967-1968, when rather few – and often poorly standardized – CBCs were made there (Appendix 3). Successive lows seemed more frequent in CBCs in Nova Scotia, Prince Edward Island and insular Newfoundland (Appendix 3), probably because not all southward irruptions brought redpolls to those more peripheral areas by December.

Without a seed-set "cycle" inherent in the food-trees, which may "take over" after interruptions, biennial periodicity of redpoll exodus would be expected to break down for years at a time, as noted by Larson and Bock (1986). Atlantic Canada redpoll data also suggested that such interruptions – and later resumptions – of high-low alternation indeed occurred here several times in the last 70 years. Some of those irregularities occurred during the 1920-1950 period when Larson and Bock (1986) found weak or no evidence of alternating peaks and lows in redpoll numbers on CBCs in northeastern and north-central states. Irruptions on a "biennial cycle" in a seasonal environment can vary towards shorter length only by becoming annual occurrences. As remarked, some redpolls come to southern New Brunswick every winter, though numbers that come here vary greatly between winters.

Winter distribution of redpolls within the Atlantic Provinces

Why is southern New Brunswick more attractive to redpolls than other Atlantic Canada wintering areas? Food-tree availability might be greater, but those tree species are very common all across the Atlantic region,

in early stages of forest succession (Loucks 1962). Most of northern New Brunswick remained under (mostly conifer) forest cover throughout European settlement, but large parts of southern New Brunswick were cleared for agriculture but later abandoned (compare D. S. Erskine 1968). Recent dominance of birches or alders in S–NB forests may be related both to succession (time since field abandonment) and prior use (reduction of seed-sources for other tree species). Compared to S–NB and Bord, most abandonment of agricultural lands in Prince Edward Island occurred after World War 2, and much old-field succession there led directly to spruces (AJE observations). In Nova Scotia, much agricultural land abandonment was underway before 1900 (D.S. Erskine 1968), with very slow forest regrowth. In Newfoundland, agriculture was always minimal. Thus southern New Brunswick may provide larger areas of suitable food trees (birch and alder) for redpolls than other parts of the Atlantic Provinces.

Routes between breeding and wintering areas

Redpolls arrive in wintering areas from breeding areas somewhere to northward of each observation site, but unambiguous evidence connecting breeding and wintering areas of individuals is lacking. Apparent NW–SE or WNW–ESE movements suggested by *indirect* banding returns (Troy 1983; Brewer et al. 2000) seem rather to be artifacts of human distribution, with redpolls often using different areas during successive irruptions (Hochachka et al. 1999). Only one indirect recovery – a bird banded at Quebec City March 1956, and recovered in Alaska June 1957 – links a Canadian wintering area with any area in breeding season. Other band returns linking Alaska to areas east of the Great Lakes (Brewer et al. 2000), plus the scarcity of wintering redpolls in the United States west of the Rockies (Bock and Lepthien 1976), suggest that redpolls breeding in Alaska mostly move southeasterly, but that pattern need not be general. Redpolls breeding in Labrador and Ungava evidently do not move southeasterly (= out to sea!). Without contrary evidence, it is plausible to assume that most wintering redpolls originate somewhere in a northward sector with apex at the observation site, with those wintering in the Atlantic Provinces mostly coming from Labrador or Ungava.

Hochachka et al. (1999) thought Project FeederWatch data in their "Maritime" region (which included all of Quebec!) suggested redpoll movements thither from farther west between November and January. Data from within the Maritimes (as discussed herein) are unsuitable for examining that possibility. The absence of any redpoll band returns between the Atlantic provinces and more western areas may reflect only the scarcity of passerine banders in the Maritimes. Redpolls that breed in Labrador might move to the southwest, bypassing the Maritimes – as do some Labrador-breeding birds that are scarce here except in western New Brunswick, e.g., White-crowned Sparrow (*Zonotrichia leucophrys*; AJE data). However, redpolls appear here in numbers frequently, and it seems more plausible that Labrador birds move here directly.

A few CBC "outliers" suggested that redpolls from Labrador sometimes might move to New Brunswick via insular Newfoundland and eastern Nova Scotia. The huge count at St. Anthony in December 1976 was in a winter when only one other CBC in the region (also in INF) found >100 redpolls. Most other large counts (>400 unadjusted) in eastern Nova Scotia and Newfoundland occurred in 1968-69, winter of the most widespread regional invasion. Exceptionally high counts probably represented wandering flocks rather than movements within an invasion. The generally low redpoll numbers found in Newfoundland, and the species' frequent absences across much of Nova Scotia, argue against regular movement from Labrador to New Brunswick by way of Newfoundland.

Redpolls moving southward from Labrador and eastern Ungava probably cross the Gulf of St. Lawrence directly, as do many other migrating birds (also based on circumstantial evidence). Birds engaging in long overwater flights may be displaced by strong winds, which are frequent in the Gulf region. The strongest sustained winds in December 1991 at Moncton, New Brunswick (24-hr mean 28km/hr, gusts to 45 km/hr, from west) occurred on the day preceding the huge flight of redpolls on Cape Tormentine CBC that year; that count seemingly detected the return westward of a major redpoll movement that had been displaced eastward by those winds. The few very high counts in southern sub-regions of the Maritimes, where redpolls are less frequent, may include "overflights", carried by strong tail-winds beyond usual destinations in southern New Brunswick.

We suggest that irregular abundance but near-annual occurrence of redpoll visitation, in the Atlantic Provinces, explains observed observations better than attempts to find periodicity in their irruptions.

Acknowledgments

We thank the many observers who contributed to regional CBCs over many years. John Chardine read and commented helpfully on an advanced draft of this article. Julie Sircom and Stefen Gerriets prepared the figures. The MS was prepared while AJE worked under an Emeritus appointment by Canadian Wildlife Service, Atlantic Region, Environment Canada, which provided computer, library, and office facilities. Stuart Houston and an anonymous reviewer provided helpful reviews of the submitted MS.

Literature Cited

Bock, C. E., and **L. W. Lepthien.** 1976. Synchronous eruptions of boreal seed-eating birds. American Naturalist 110: 559–571.

Brewer, D., A. Diamond, E. J. Woodsworth, B. T. Collins, and **E. H. Dunn**. 2000. Canadian atlas of bird banding. Volume 1: Doves, cuckoos, and hummingbirds through passerines, 1921–1995. Special Publication/Canadian Wildlife Service, Environment Canada. 394 pages.

Bryson, R. 1966. Air masses, streamlines, and the boreal forest. Geographic Bulletin 8(3): 228–269.

Cadman, M. D., P. F. J. Eagles, and **F. M. Helleiner**. 1987. Atlas of the breeding birds of Ontario. Federation of Ontario Naturalists and Long Point Bird Observatory, University of Waterloo Press, Ontario. 617 pages.

Cyr, A., et **J. Larivée**. 1995. Atlas saisonnier des oiseaux du Québec. Presses de l'Université de Sherbrooke et Société de loisir ornithologique de l'Estrie, Sherbrooke, Québec. 711 pages.

Erskine, D. S. 1968. The Atlantic region. Chapter 9, pages 231–280 *in* Canada: A geographic interpretation. *Edited by* J. Warkentin. Toronto, Methuen.

Gauthier, J., and **Y. Aubry**. *Editors*. 1996. The breeding birds of Québec. Atlas of the breeding birds of southern Québec. Association québécoise des groupes ornithologiques, Province of Quebec Society for the Protection of Birds, Canadian Wildlife Service – Quebec Region. 1302 pages.

Godfrey, W. E. 1986. The birds of Canada. Revised edition. National Museum of Natural Sciences, Ottawa. 595 pages.

Hochachka, W. M., J. V. Wells, K. V. Rosenberg, D. L. Tessaglia-Hymes, and **A. A. Dhondt**. 1999. Irruptive migration of Common Redpolls. Condor 101: 195–204.

Houston, C. S., M. I. Houston, and **A. R. Smith**. 2000. Biennial redpoll invasions. Blue Jay 58: 116–124.

Keith, L. B. 1963. Wildlife's ten-year cycle. University of Wisconsin Press, Madison. 201 pages.

Kennard, J. H. 1976. A biennial rhythm in the winter distribution of the Common Redpoll. Bird-Banding 47: 231–237.

Larson, D. L., and **C. E. Bock**. 1986. Eruptions of some North American boreal seed-eating birds. Ibis 128: 137–140.

Loucks, O. L. 1962. A forest classification for the Maritime Provinces. Proceedings of the Nova Scotia Institute of Science 25: 85–167.

Newton, I. 1972. Finches. New Naturalist series. Collins, London. 288 pages.

Smith, A. R. 1996. Atlas of Saskatchewan birds. Saskatchewan Natural History Society, Special Publication number 22. 456 pages.

Todd, W. E. C. 1963. Birds of the Labrador peninsula. Carnegie Museum, Pittsburgh, Pennsylvania and University Toronto Press, Ontario. 819 pages.

Troy, D. M. 1983. Recaptures of redpolls: movements of an irruptive species. Journal of Field Ornithology 54: 146–151.

Received 23 October 2002
Accepted 20 November 2003

Appendix 1. Christmas Bird Counts (CBCs, latitude-longitude of centre given) used in redpoll study in Atlantic Provinces, grouped by sub-regions (defined in text, also see Figure 1).

Northern New Brunswick (N–NB)	
Kouchibouguac National Park	46°49'N, 64°55'W
Miramichi	47°00'N, 65°34'W
Mount Carleton	47°23'N, 66°53'W
Nictau	47°14'N, 67°09'W
Perth–Andover	46°45'N, 67°42'W
Plaster Rock	46°54'N, 67°24'W
Southern interior New Brunswick (S–NB)	
Cambridge–Narrows	45°50'N, 65°57'W
Fredericton	45°55'N, 66°35'W
Florenceville	46°27'N, 67°38'W
Fundy National Park	45°36'N, 65°01'W
Hampton	45°32'N, 65°51'W
Hartland	46°18'N, 67°32'W
Jemseg	45°52'N, 66°10'W
Moncton	46°05'N, 64°37'W
Riverside–Albert	45°45'N, 64°44'W
Woodstock	46°09'N, 67°35'W
South coastal New Brunswick (ScoNB)	
Eastport–Campobello	44°50'N, 66°55'W
Grand Manan Island	44°41'N, 66°48'W
Lepreau	45°09'N, 66°27'W
Saint John	45°18'N, 66°06'W
St. Andrews	45°05'N, 67°03'W
N.B.–N.S. border area (Bord)	
Amherst, N.S.	45°44'N, 64°15'W
Cape Tormentine, N.B.	46°07'N, 63°55'W
Sackville, N.B.	45°53'N, 64°22'W
North and east Nova Scotia and Prince Edward Island (N–NS/PE)	
Hillsborough, P.E.I.	46°08'N, 63°02'W
Montague, P.E.I.	46°05'N, 62°35'W
Prince Edward Island National Park	46°23'N, 63°08'W
Cape Breton Highlands National Park, N.S.	46°43'N, 60°23'W
Glace Bay, N.S.	46°13'N, 59°57'W
Springville, N.S.	45°27'N, 62°38'W
Southern Nova Scotia (S–NS)	
Brier Island	44°16'N, 66°29'W
Broad Cove	44°14'N, 64°27'W
Halifax (east) *	44°41'N, 63°23'W
Halifax (west) *	44°34'N, 63°38'W
Halifax–Dartmouth	44°36'N, 63°29'W)
Kingston	44°59'N, 64°57'W
Shubenacadie	45°05'N, 63°24'W
Wolfville	45°03'N, 64°23'W
Insular Newfoundland (INF)	
Bonne Bay	49°31'N, 57°53'W
Corner Brook	48°57'N, 57°50'W
Cape Race	46°44'N, 53°09'W
Cape St. Mary's	46°52'N, 54°05'W
St. Anthony	51°24'N, 55°35'W
St. John's	47°33'N, 52°42'W
Terra Nova National Park (north)	48°38'N, 53°54'W

*these two counts replaced, after 1993, by the next count.

Appendix 2. Redpoll data from Memramcook (McManus) and Sackville (Erskine), New Brunswick, by winter.

Irruptions expected in OE winters). Only last two digits of years shown (1928–2002). For each winter are given: month–number(s) when redpolls noted (12=December, 1=January, etc.), total dates with redpolls, maximum/day (with month–number of maximum – omitted when only seen in one month). (Note: "none in notes" means none identified; "no notes" means expectable period of "flight" was missed).

Odd–Even (OE) winters		[Even–Odd (EO) winters]	
		[28–29]	1, 1d, mx1+
29–30	none in notes	[30–31	none in notes]
31–32	3, 1d, mx1	[32–33]	11, 3d, mx25
33–34	no notes Nov–Mar	[34–35	none in notes]
35–36	11, 2d, mx5+	[36–37	no notes all winter]
37–38	12, 1d, mx11	[38–39	only 1 note Nov–Feb, none]
39–40	no notes all winter	[40–41]	12–3, 16d, mx15(2)
41–42	12,3, 7d, mx50(3)	[42–43	no notes all winter]
43–44	11,12,5, 25d, mx50(11)	[44–45]	2, 2d, mx2
45–46	notes only 28 Mar, none	[46–47]	12–4, 68d, mx200(3)
47–48	10,2–4, 12d, mx25(2)	[48–49]	10–4, 64d, mx100+(3,4)
49–50	10–4, 29d, mx100(3)	[50–51]	1, 2d, mx1
51–52	notes only 14–16 Nov, none	[52–53]	11–4, 111d, mx150(3)
53–54	notes only 7 d, none	[54–55]	3, 3d, mx25
55–56	notes only 2 d, none	[56–57]	2, 1d. mx1
57–58	11–2,4, 37d, mx750(1)	[58–59	no notes all winter]
59–60	12–5, 28d, mx300+(12)	[60–61	no notes all winter]
59–60	4, 1d, mx40	[60–61	none seen or hd]
61–62	10–4, 15d, mx20(11)	[62–63	none in notes]
61–62	12–2, 6d, mx23(12)	[62–63]	3, 1d, mx10
63–64	12,2–3, 4d, mx300(3)	[64–65]	11–2, 6d, mx2(11)
63–64	12, 1d, mx3	[64–65]	12–1, 5d, mx42(12)
65–66	11,2–4, 12d, mx84(12)	[66–67]	12,1,3, 4d, mx10(12)
65–66	10,12,3–4, 6d, mx18(3)	[66–67]	12,3. 2d, mx8(12)
67–68	none in notes	[68–69]	10–4, 85d, mx120+(12)
67–68	none seen or hd	[68–69	11–12, 6d, mx25(12)
69–70	10–4, 42d, mx122(2)	[70–71	none in notes]
71–72	9–4, 40d, mx100s(1)	[72–73]	10,2, 2d, mx 13(10)
73–74	2,3, 2d, mx30(3)	[74–75	none in notes]
75–76	notes only 1–29 Mar, none	[76–77	no notes all winter]
77–78	no notes all winter	[78–79	no notes all winter]
77–78	12–1,3, 3d, mx17(1)	[78–79	none seen or hd]
79–80	no notes all winter	[80–81]	11, 1d, mx6
79–80	none seen or hd	[80–81]	12,3–4, 8d, mx25(3)
81–82	12, 1d, mx64	[82–83	no notes all winter]
81–82	12–1,3–4, 8d, mx35+(4)	[82–83	none seen or hd]
83–84	12–1,3, 4d, mx83(12)	[84–85	none seen or hd]
85–86	3, 1d, mx1	[86–87	no notes all winter]
85–86	11–12,2–3, 6d, mx10(11)	[86–87]	12–2, 10d, mx51(2)
87–88	11–2, 8d, mx31(12)	[88–89	none seen or hd]
89–90	1, 1d, mx15	[90–91]	4, 1d, mx2
91–92	11–2, 11d, mx325+(12)	[92–93	none seen or hd]
93–94	11,1, 6d, mx 40	[94–95	no notes all winter]
93–94	11–4, 35d, mx40+(3)	[94–95	none seen or hd]
95–96	12–3, 9d, mx10(1)	[96–97	none seen or hd]
97–98	11–3, 20d, mx40+(12,3)	[98–99]	11, 1d, mx5
99–00	11–3, 38d, mx58+(12)	[00–01	none seen or hd]
01–02	11–4, 72d, mx86+(1)		

Appendix 3. Summary of Atlantic Provinces Redpoll CBC data

For each winter (dated by start year, 2 digits), data are grouped geographically: N–NB, S–NB, ScoNB; Bord; N–NS/PE, S–NS; INF (see text for area definitions, also Figure 1); for each five-year series, maximum numbers of circles counted in any one year in each group are shown; within each group and year, numbers shown are: number of counts with 0 redpolls; number of counts with >=50 birds; highest count (latter two figures adjusted to birds/10 party-hours). (n.d.) = data missing.

Yr	N–NB	S–NB	ScoNB	Bord	N–NS/PE	S–NS	INF
		Maximum number of CBCs used in each region 1960–1964					
	0	5	3	3	2	4	0
60		2,0,2	3,0,0	1,0,0	1,0,0	2,0,15	
61		1,2,107	1,1,25	1,1,92	1,0,0	3,0,0	
62		3,0,9	2,0,0	2,0,	11,0.0	4.0,0	
63		2,0,6	3,0,2	2,0,3	(n.d.)	2,0,0	
64		1,0,35	3,0,0	0,0,28	2,0,0	3,1,200	
		Maximum number of CBCs used in each region 1965–1969					
	2	6	4	3	3	5	2
65		1,3,131	3,0,10	0,2,77	1,0,4	1,0,9	
66		3,0,5	2,0,4	2,0,5	2,0,0	3,0,<1	1,0,0
67		3,0,1	2,0,4	3,0,0	3,0,0	2,0,14	1,0,0
68		0,5,695	0,3,106	0,2,107	0,1,278	0,5,270	0,2,163
69	0,0, 27	0,3,173	0,2,667	0,2,88	1,0,11	2,1,83	1,0,8
		Maximum number of CBCs used in each region 1970–1974					
	5	9	5	3	5	7	4
70	1,0, 0	5,0,3	4,0,<1	2,0,<1	2,0,<1	2,0,2	2,0,0
71	1,0, 10	0,4,210	0,1,125	0,1,52	0,2,59	3,0,28	2,0,<1
72	3,0, 10	3,0,19	4,0,8	1,0,8	4,0,19	2,0,15	2,0,1
73	2,1, 85	3,3,77	3,0,4	2,0,26	3,0,15	6,0,8	2,1,130
74	4,1, 53	4,0,22	4,0,0	3,0,0	4,0,0	5,0,2	2,1,91
		Maximum number of CBCs fused in each region 1975–1979					
	6	9	5	3	5	7	6
75	1,1, 71	0,4,111	1,0,19	0,2,105	1,0,14	3,1,80	2,0,<1
76	1,0, 40	2,0,33	0,0,12	1,0,14	4,0,2	2,0,6	2,2,1110
77	1,1, 75	1,4,289	1,3,167	0,0,49	4,0,26	3,0,38	2,0,23
78	0,4, 109	1,1,129	2,0,3	2,0,16	5,0,0	5,0,17	3,1,50
79	3,0, 26	4,0,7	2,0,27	2,0,6	5,0,0	7,0,0	3,0,8
		Maximum number of CBCs used in each region 1980–1984					
	6	9	5	3	6	7	7
80	1,1, 250	0,4,117	0,1,72	0,0,44	3,0,39	1,2,74	4,0,13
81	2,2, 217	0,7,456	1,2,70	0,2,186	2,2,84	1,3,163	0,0,35
82	3,0, 8	4,0,20	5,0,0	2,0,2	6,0,0	3,1,98	3,0,8
83	2,1, 75	3,0,20	1,1,55	1,1,98	4,0,12	4,0,21	1,0,36
84	5,0, 2	5,0,12	4,0,0	1,0,11	6,0,0	6,0,1	4,0,20
		Maximum number of CBCs used in each region 1985–1989					
	6	10	5	3	6	7	6
85	1,1, 125	0,4,262	1,0,11	0,2,97	2,1,170	1,0,30	0,2,96
86	0,5, 274	0,5,501	0,0,33	0,2,90	1,1,171	1,4,163	1,0,11
87	1,3, 109	1,4,808	3,0,10	0,2,100	5,0,0	6,0,<1	1,0,17
88	2,0, 23	4,0,31	4,0,<1	1,0,10	4,0,4	7,0,0	3,0,<1
89	4,1, 57	1,3,122	4,0,17	1,0,35	2,0,36	2,1,105	4,0,<1
		Maximum number of CBCs used in each region 1990–1994					
	6	10	5	3	6	6	6
90	2,1, 308	4,0,16	5,0,0	3,0,0	6,00	5,0,<1	5,0,1
91	1,3, 311	0,5,301	0,0,24	0,3,3540	2,2,394	3,1,50	0,0,17
92	4,0, 43	7,0,15	4,0,15	3,0,0	6,0,0	5,0,<1	4,1,53
93	1,1, 70	0,5,693	0,0,22	0,2,55	0,3,120	0,1,380	1,1,43
94	4,0, 7	3,1,65	3,0,<1	2,0,3	3,0,14	4,0,3	5,0,2
		Maximum number of CBCs used in each region 1995–1999					
	6	10	5	3	5	6	6
95	0,2, 174	0,7,204	2,0,41	0,0,25	1,2,108	1,1,75	1,0,8
96	3,1, 53	6,0,18	5,0,0	3,0,0	3,1,73	5,0,1	4,0,28
97	0,3, 125	0,6,313	2,0,10	0,1,67	0,4,431	0,4,278	0,0,9
98	4,0, 34	3,0,22	4,0,30	3,0,0	5,0,0	6,0,0	4,1,82
99	1,2, 136	0,8,422	0,1,172	0,3,158	0,4,699	1,2,1253	0,0,43
		Maximum number of CBCs used in each region 2000–2001					
	6	9	5	3	6	6	0
00	3,0, 18	6,0,28	4,1,80	1,0,8	3,0,3	6,0,0	n.d.
01	0,4, 107	0,5,104	1,0,12	0,1,105	0,2,95	0,4,330	n.d.

Methods for Capturing Free-Ranging Black Bears, *Ursus americanus*, in Difficult Locations

JOHN E. MCDONALD, JR.

Department of Natural Resources Conservation, University of Massachusetts, Amherst, Massachusetts 01003 USA
Present address: Division of Federal Assistance, United States Fish and Wildlife Service, 300 Westgate Center Drive, Hadley, Massachusetts 01035 USA

McDonald, John E., Jr. 2004. Methods of capturing free-ranging Black Bears, *Ursus americanus*, in difficult locations. Canadian Field-Naturalist 117(4): 621-625.

Long-term research or monitoring studies involving radiomarked Black Bears (*Ursus americanus*) conducted in areas with high human and road densities may require that radiocollars be replaced or bears recaptured for other purposes. The use of trained bear hounds is particularly suited to recapturing specific bears. However, in certain situations, hounds may not be used safely or bears may seek refuge in difficult locations. Effectiveness of two methods to capture bears via remote darting and chemical immobilization are described: (1) stalking and rushing females with cubs; and (2) allowing treed bears to descend. Both methods rely on assumptions about Black Bear behavior. Nine captures of eight individual bears are discussed; one bear drowned after being immobilized, and all others survived >5 months after capture.

Key Words: Black Bear, *Ursus americanus*, capture, immobilization, stalking, Massacheusetts.

Researchers have employed a variety of techniques to capture Black Bears (*Ursus americanus*). Common and effective techniques for initial captures include the use of Aldrich foot snares (Johnson and Pelton 1980), culvert traps (Erickson 1957) and trained hounds (Elowe 1990). Visitation of the dens of previously radiomarked animals is often employed in bear research to document reproduction and cub survival take physical measurements, and to replace or remove radiocollars. Yearling bears denned with their radiocollared mother can be fitted with collars as well. The choice of capture technique is often dictated by resources available, the study area location and terrain (e.g., for culvert traps), legal restrictions (e.g., for hounds), skill of personnel, availability of radiomarked animals (for den visits), and human use of the study area. No technique is applicable to every situation and a variety of problems can arise with each.

Culvert traps and foot snares simplify the immobilization process because the bear is confined either within the culvert trap or restricted to a small radius of movement by the snare. Snares may not be the method of choice in areas of high human use where the physical security of both captured bears and the public is at risk. Culvert traps may be difficult to use in areas far from roads. Den visits are relatively straightforward; under ideal conditions the bear remains in the den when approached and the researcher is able to immobilize it *in situ*. In less than optimal conditions, the bear vacates the den and the researcher must attempt to recapture the bear another day. In other cases, the den is difficult to enter; this is often the case for tree dens (Godfrey et al. 2000). Except in rare circumstances, however, den visits involve recapturing bears that were previously captured and radiocollared by other means.

Trained hounds allow researchers the ability to seek out bears that may be difficult to capture through trapping, either because they are in remote areas or are trap-shy. Hounds are also useful to recapture specific radiocollared bears. By radiotracking the target individual and moving to a close proximity such that the hounds have the bear's trail before they are released, researchers can often recapture specific bears (Fuller 1993). Individual bears vary in their response to hounds; not all chases result in a capture or the capture of the target individual, but in many instances the chase ends with a treed bear. However, the task remains to immobilize the bear and retrieve it from the tree. Usually, this is accomplished by darting the treed bear and allowing it to fall from the tree into nets; sometimes the bear does not fall from the tree and the researcher must climb the tree and lower the bear to the ground.

In Massachusetts, I employed all of the techniques mentioned above and all were successful (McDonald 1998). Part of my research involved recapturing radiocollared females with cubs during the late spring to obtain milk samples. Many other bears fled their dens when approached during the winter and needed to be captured when active in the spring in order to replace their radiocollars. Hounds were the method of choice for capturing these bears because of the ability to target specific bears. However, many of the bears in my study frequented areas on the fringe of or in the midst of towns. In these developed areas, the high road and housing densities sometimes precluded the use of hounds to capture specific bears or the hounds were not available.

Another problem that I encountered when using hounds was the choice of tree in which the bear sought refuge. Many bears treed in multi-stemmed Eastern

White Pines (*Pinus strobus*) that posed certain risks. The main concern was that an immobilized bear would fall into one of the many forks or crotches of the tree rather than falling to the outside and into the net. Other bears chose trees under which we could not set nets, because of the steepness of the terrain or a lack of nearby trees to which we could fasten the net. Given the effort expended to chase and tree these bears, and my desire to harass them as little as possible, I was reluctant to abandon the capture attempt and in collaboration with my field crew developed a simple method to capture bears in these situations.

This paper describes two techniques for immobilizing free-ranging bears in difficult circumstances. The techniques are variants of each other. The first method is specific to the capture of radiocollared female bears with cubs. The second method can be used with any treed bear.

Study Area

My study was conducted in western Massachusetts (42° 27' N, 72° 41' W) on the 150- km^2 Conway-Williamsburg study area (CWSA). The CWSA was 70% forested and >90% privately owned with elevations ranging from 30 m to 450 m (Fuller 1993). Hardwood dominated forests consisted of Northern Red Oak (*Quercus rubra*), Red Maple (*Acer rubrum*), Black Birch (*Betula lenta*), Sugar Maple (*A. saccharum*), and hickories (*Carya* spp.). Major softwoods were Eastern White Pine and Eastern Hemlock (*Tsuga canadensis*).

Corn was the major agricultural crop present in the CWSA. Usually between 10 and 20 cornfields were present in the CWSA each year, ranging in size from 0.4 to 4.0 ha. Other human-related food sources included apiaries, apple orchards, and home bird feeders. Human densities in the study area ranged from 18/km^2 to 459/km^2 (Horner 1996). Road density in Massachusetts Deer Management Zone 4N, which contained the study area, was 1.77 km/km^2 (W. A. Woytek, Massachusetts Division of Fisheries and Wildlife, personal communication). However, in areas around town centers and the city of Northampton road density was higher.

Methods

Initial Capture and Handling

I captured female bears between 1993 and 1998 using foot snares and trained bear hounds; some bears were originally captured during previous research (Elowe 1984; Fuller 1993) or were captured as yearlings in winter dens with their mother. I immobilized bears using a mixture of ketamine hydrochloride (10-17 mg/kg body weight) and xylazine hydrochloride (1-2 mg/kg body weight) or a mixture of tiletamine hydrochloride and zolazepam hydrochloride (i.e., Telazol; 3.9-7.3 mg/kg body weight). I found that a standard dose of 300 mg of Telazol was sufficient to safely immobilize most free-ranging adult female bears, regardless of body weight.

Recapture Techniques for Radiocollared Females with Cubs

To obtain milk samples from free-ranging female bears with cubs, I attempted to recapture them during late May and early June, 1994–1996. Most were recaptured using trained hounds as described above. However, several adult females were located in areas with high road densities or among homes; usually the bear would be in a small wetland area abutted by homes. My judgement was that these were inappropriate settings to attempt to chase the bear with hounds due to the risk of the bear and hounds crossing heavily traveled roads or causing too much general commotion in developed areas (i.e., treeing in a front yard). At other times, the bear may have been in a remote area but the hounds were not available when I needed to capture a specific bear to remain within my sampling window. In both of these circumstances, if I elected to try to capture that specific bear in that situation I employed a stalking technique that required a minimum of two people equipped with dartguns and two-way radios.

I radiotracked the bear and when I determined we were within about 100 m (based on signal strength or sighting the bear) of the bear we attempted to close in as quickly as possible. If we could see the bear we would rush toward it. The objective was to get the female to put the cubs up a tree (cub tree) that we could identify, either by seeing the cubs or hearing them climb the tree. If we could identify the cub tree, we would get to it as quickly as possible, making noise to let the female know where we were. After several minutes of observation of the site, one person with a dart gun would take up a position within 15 m of the cub tree, the other person or people would then noisily walk away in a direction roughly perpendicular to the female as determined either visually or by the radio signal. The objective here was to persuade the female that all of her pursuers had left the cub tree and it was safe to return. When she did return, the hidden person would attempt to dart her. If darting was successful, the bear would run off and would be located by radiotracking.

In practice, several outcomes may present themselves with this technique: (1) the cubs tree and the female departs, (2) the adult bear trees with the cubs, (3) the cubs tree and the female holds her ground at the base of the tree or bluff charges the pursuers, (4) the cubs tree, the female departs, but the cub tree is not identified, and (5) all bears depart. The first outcome is as discussed in the technique description above. If the adult trees with the cubs, then she can simply be handled like any treed bear, providing the appropriate equipment (i.e., nets and ropes) is available. If the female holds her ground at the cub tree, the situation becomes more difficult. Some females

would allow us to approach within darting range (20 m) and it was tempting in such instances to simply dart the female. However, there was a risk that when darted the female would climb the cub tree. At that point, there would only be 5 to 15 minutes to set up nets before she became immobilized and fell. Bears that charged usually would not climb the cub tree; these bears could be darted when they stopped their charge and could be treated as in situation 1.

In some instances, a female would put her cubs up a tree when we were a long distance off and then she would depart. In those cases, if the cubs climbed into the canopy of the tree, especially Eastern White Pines or Eastern Hemlocks, we could not locate them. At this point we would simply leave the area. In other instances, the cubs were quite large (>10 kg) by the time we were trying to capture them and instead of treeing would simply move off with the female. If we determined this to be the case we would leave the area.

Treed Bears in Difficult Locations

For bears chased with hounds that eventually treed, the tree itself sometimes posed risks to safe capture by means of chemical immobilization. As described above, many bears sought refuge in multi-stemmed trees that posed serious injury risks to immobilized bears that might fall into a fork or strike another stem. Other bears sought refuge in otherwise suitable trees but were too high (or behind thick screening, especially in hemlock trees) to dart. For bears in otherwise suitable trees, we would first attempt to get the bear to change position, thus offering a shot, by repeatedly and rapidly striking the tree with hand-held rocks, clubs cut on site, or whatever suitable equipment we had (e.g., small shovels or the back of an axe). This noise and vibration frequently caused bears to move around in the tree and often resulted in our being able to dart them. Sometimes striking the tree caused the bear to descend and leave the tree, and we could dart it.

However, in some instances with both unsuitable and suitable trees, we could not safely dart the treed bear. In this case we would employ a variation of the method described above for adult females. One or two people equipped with dart guns would hide within 15-m of the tree. When these people were hidden, the other people on site would noisily leave with the dogs and all the equipment. When the departing crew members were away from the tree, the bear would descend and could be darted on the ground. The bear would then leave the site and be located by radio-tracking when immobilized. This technique could be employed on bears with existing radiocollars. Barbed, transmitter darts allowed the method to be used to locate immobilized bears not previously radiocollared. Uncollared immobilized bears were also found by using a leashed hound to locate them.

Results

Radiocollared Females with Cubs

I captured four individual females with cubs five times using the track and rush method. One female was captured by this method in two different years. Three additional stalking attempts were unsuccessful; one of these females was subsequently captured several days later using this method, one was later captured with hounds, and no attempt was made to recapture the other. In one case the female held her ground and I darted her; she subsequently treed with the cubs and fell about 8 m to the ground after immobilization. I did not detect any physical injuries from the fall; she recovered and survived for >4 years. Two females treed with their cubs and were darted in the tree; nets were erected under both trees. One bear descended after being darted and became immobilized <100 m from the tree; the other became immobilized in the tree and I climbed up and lowered her to the ground with a rope. Two other bears were tracked and rushed and the cub trees identified. Both were darted on the ground when they returned to the cub tree after the second person had departed. Both were recovered within 50 m of the cub tree. I did not keep an accurate record of the time between the departure of the second person and the bear's return, but in both cases it was less than 10 minutes.

One of the failed stalks was the first attempt and the person hiding by the cub tree climbed a nearby tree and may have been visible to the bear. The second person in this attempt did not completely move out of the area, but moved noisily away and then was able to watch the bear with binoculars. After about 45 minutes of waiting, we abandoned the attempt. In another failed attempt, I was unable to locate the cub tree and the female moved off. This bear was later recaptured with hounds. In the final failed stalk, four people were involved and instead of completely leaving the area several of them stayed too close to the cub tree and the female would not return. This bear was captured by stalking several days later using only two people.

No bears died during handling with this method. One female was killed as a nuisance bear five months after capture and I could not determine the fate of her cubs. A second female and her cub were both killed during the hunting season four months after capture (her other cub had been killed by a vehicle prior to the stalk and capture event). One female that was captured twice by this method had three cubs during the first capture in 1994, two of which were present in her den the following winter; the next time (1996; this was the occasion during which she fell from the tree) she had two cubs, both of which were present in her den the following winter. The other female had three cubs when captured and could not be captured

in the den the following winter but snow-tracking indicated that at least two of the three cubs were with her at that time. The lone bear not recaptured after a failed stalk rejoined her three cubs and all were present in the den the following winter.

Bears in Difficult Trees

I captured four individual bears (one in 1994, three in 1996) by hiding near the tree and having the crew and dogs leave. One of these bears, a female that treed with a yearling in 1994, drowned after being darted. I darted her as she left the tree; the bear ran about 150 m before becoming immobilized with her head under water in a small stream (about 2 m wide and <0.5 m deep). I located her <20 minutes after darting and tried mouth-to-nose resuscitation but could not revive her. The other three bears were recovered within similar distances and all survived ≥3 years after capture. Again, I did not record the time from crew departure to bear darting but I was present as shooter in all instances and all four bears descended <5 minutes after the crew was out of sight of the tree. In one instance the bear treed within sight of our vehicles, although >100 m away, and would not descend until the last vehicle departed. Within 1 minute of that vehicle departing, the bear descended. One additional bear, not included in the tally above, treed after fleeing her den during the winter. I employed the same technique of hiding a shooter near the tree and the rest of the crew moved off and hid. This bear was darted when still about 6 m up the tree; she climbed back up the tree, became immobilized and fell about 10 m to the ground. The ground was covered with about 1 m of snow and the bear recovered, had cubs the following winter, and survived until being taken during the hunting season 18 months later.

As stated above, the three bears captured during 1996 all survived >3 years after capture. At the time of capture (2 June) one of the three appeared to have already lost the entire litter of cubs (n=2) she had during the winter; her nipples were small and we could not express any milk from her, even after injection of 100 IU of oxytocin. All of the cubs from the other two females (one litter of two and one litter of three) were present as yearlings in their 1997 dens.

Discussion

The methods I used to capture bears in difficult settings allowed me to minimize the risks associated with hound pursuit in a roaded area and the number of times we had to harass individuals to perform research tasks. The one mortality was due to my judgement that it was better not to immediately chase the darted bear and to allow 10 minutes for her to become immobilized before tracking. That mortality was especially regretful as only the bear's head was under water, not even up to its ears, and the stream was the only water source within 0.5-km of the tree. After that event, we pursued bears darted on the ground as quickly as possible, remaining at a distance where we could see them and ensure their safety.

It was important that all crew members leaving the bear tree moved off quickly and noisily and did not try to take up a position where they could watch the bear descend the tree because the bear would not descend if it could see or hear people and dogs. Departing crew members need to keep their radios on to receive instructions from the shooter(s) about the need to move farther off, as in the above case with the vehicles, or to return to help pursue the darted bear. Conversely, the shooter's radio should be off unless they need to initiate contact. Patience was required to overcome the temptation to dart the bear while it was still in the tree. In my experience, the descending bear would pause at the bottom of the tree and look around before moving off; that was the time to dart it.

More judgement was required when darting females returning to the cub tree. This technique relies on the basic tolerance and low degree of aggressiveness of Black Bears (DeBruyn 1999: 76). Certainly, every individual bear will behave differently and I have tried to present the types of responses that can be expected. There are two premises to this technique: (1) adult female bears can not count and will observe the departing crew and think that all have left; and (2) the adult female will not be overly aggressive and attempt to contact the crew at the cub tree. The latter was my experience and therefore we never carried firearms for deterrence. Some bears would bluff charge, but all stopped short of contact (this included bears I encountered with cubs at other times, too).

Wind direction did not appear to influence the female's approach. The bear could often be observed circling in the distance while crew members were at the cub tree. I relied on the fact that the bear would observe the departing crew and would then feel comfortable about approaching the tree, regardless of human scent. However, the hidden shooters wore dark or drab clothes to minimize the risk of returning or descending bears spotting them.

The method of capturing radiocollared females with cubs obviously has limited utility. But, as more bears live in highly populated regions and biologists are required to do research on basic life history parameters in order to justify management actions, there will be times when this method can be useful. Given the availability of radio-equipped darts and non-narcotic drugs that can immobilize adult bears with small volumes (e.g., Telazol) I think the method described for treed bears will have a wider application.

Acknowledgments

Funding for this research was provided by the Massachusetts Division of Fisheries and Wildlife through Federal Aid in Wildlife Restoration Project W-35-R, the

Massachusetts Cooperative Fish and Wildlife Research Unit, and the Department of Natural Resources Conservation, University of Massachusetts, Amherst. I thank T. Fuller for the opportunity to work on the project. D. Fuller, W. Woytek, E. Howard, and A. Howard provided advice, expertise, and acted in various roles in the field, including as shooters. D. Luke and T. Russell provided and handled trained bear hounds.

Literature Cited

DeBruyn, T. D. 1999. Walking with bears. The Lyons Press, New York, USA.

Elowe, K. D. 1984. Home range, movements, and habitat preferences of black bears (*Ursus americanus*) in western Massachusetts. M.Sc. thesis, University of Massachusetts, Amherst.

Elowe, K. D. 1990. Bear hunting with hounds: techniques and effects on bears and the public. Pages 101–109 *in* Proceedings of the 10th Eastern workshop on black bear research and management. Bismarck, Arkansas.

Erickson, A. W. 1957. Techniques for live-trapping and handling black bears. Transactions of the North American Wildlife Conference 22: 520-543.

Fuller, D. P. 1993. Black bear population dynamics in western Massachusetts. M.Sc. thesis, University of Massachusetts, Amherst.

Godfrey, C. L., K. Needham, M. R. Vaughan, J. H. Vashon, D. D. Martin, and **G. T. Blank, Jr.** 2000. A technique for and risks associated with entering tree dens used by black bears. Wildlife Society Bulletin 28: 131-140.

Horner, E. R., *Editor.* 1996. Massachusetts municipal profiles, 1996-97. Information Publications, Palo Alto, California.

Johnson, K. G., and **M. R. Pelton.** 1980. Prebaiting and snaring techniques for black bears. Wildlife Society Bulletin 8: 46–54.

McDonald, J. E., Jr. 1998. The effects of food supply and nutrition on black bear reproductive success and milk composition. Ph.D. Dissertation. University of Massachusetts, Amherst.

Received 6 June 2002
Accepted 30 April 2004

Black Bear, *Ursus americanus,* Denning Chronology and Den Site Selection in the Northeastern Cascades of Washington

WILLIAM L. GAINES

U.S. Forest Service, 215 Melody Lane, Wenatchee, Washington 98801 USA

Gaines, William L. 2003. Black Bear, *Ursus americanus*, denning chronology and den site selection in the northeastern Cascades of Washington. Canadian Field-Naturalist 117(4) 626-633.

I studied Black Bear denning chronology and den site selection during 1995-1998 in the northeastern Cascade Mountains of Washington. Male Black Bears entered dens between 22 October and 19 November and emerged between 4 April and 7 May. Females entered dens somewhat sooner, between 15 October and 19 November, and emerged later than males, 4 April and 22 May. These den entry and emergence dates were similar to those reported at similar lattitudes in northwestern Montana. Roads had an important influence on den site selection by Black Bears in this study area. Bears selected dens in areas with no open roads >200 ha in size, >500 m from the nearest open road, and 1500-2000 m in elevation. The combination of information on denning chronology and site characterstics should allow managers to coordinate human activities to reduce the potential for disturbance to denning Black Bears.

Key Words: Black Bear, *Ursus americanus,* northeastern Cascade Mountains, denning chronology, den site characteristics.

Black Bear *(Ursus americanus)* hibernation has been studied in many areas in North America (Aune 1994; Clark et al. 1998; Hamilton and Marchinton 1980; Hellgren and Vaughan 1989; Oli et al. 1997; Schooley et al. 1994; Smith 1985; Weaver and Pelton 1994; Wooding and Hardisky 1992). Black Bears hibernate in dens throughout their range, but the length of denning and types of dens vary among geographic regions and habitat conditions. In general, bears in southern habitats den for shorter periods than those in northern habitats where winters are longer and more severe (Smith 1985; Hellgren and Vaughan 1989; Weaver and Pelton 1994).

Hibernation in Black Bears is an energy-conserving strategy used to survive winter periods when food is limited and ambient temperatures unfavorable for efficient thermoregulation (Johnson et al. 1978; Johnson and Pelton 1980; Pelton et al. 1980; Johnson and Pelton 1981). The survival value of winter dormancy is particularly evident for Black Bears because their foraging efficiency is closely tied to seasonal plant cycles (Ewer 1973). Bears are believed to remain active prior to denning until a negative energy balance occurs (Schooley et al. 1994). During hibernation, metabolic rates of bears are reduced substantially and they do not normally eat, drink, urinate or defecate (Folk et al. 1972; Nelson et al. 1973; Nelson and Beck 1984). Parturition and early maternal care occurs in dens, and lack of adequate den sites may result in litter loss or complete reproductive failure (Hamilton and Marchinton 1980; Alt 1984; Smith 1985; Weaver and Pelton 1994). Black Bears may be at risk of being killed by predators if dens do not provide adequate protection (Paquet and Carbyn 1986; Ross et al. 1988; Smith and Follman 1993; Boyd and Heger 2000). Human disturbance has been documented to cause den abandonment, which can lead to increased winter weight loss (Tietje and Ruff 1980; Goodrich and Berger 1994). Because of these factors, Black Bears likely select dens that provide energetic efficiency and are relatively safe from predation, human or other disturbances, and weather (Oli et al. 1997).

Understanding the denning ecology of Black Bears and the influence of human activities is important for the proper development of Black Bear management plans and evaluation of the effects of human activities on Black Bear habitat (Pelton 1985; Hillman and Yow 1986; Hellgren and Vaughan 1989; Weaver et al. 1990; Linnell et al. 2000). Claar et al. (1999) and Linnell et al. (2000) identified the need to develop denning habitat models in order to manage human activities to avoid or minimize impacts to denning bears.

Although the denning ecology of Black Bears has been studied extensively in North America, few studies have investigated Black Bear denning in Washington (Poekler and Hartwell 1973; Lindzey and Meslow 1976), and no studies have been conducted on den site selection in the North Cascades of Washington. The objectives of this study were: (1) Describe Black Bear denning chronology, (2) Assess factors that influence Black Bear den site selection, (3) Develop a GIS model of potential denning habitat within the study area, and (4) Provide recommendations on the management of human activities and Black Bear denning.

Study Area

The Okanogan Study Area was located on the Methow Ranger District, Okanogan National Forest (Figure 1). Bears were captured and radio-collared in both backcountry and front-country areas. Some of the bear locations occurred in areas with limited access and were only accessible by foot. Most of the radio-collared bears are located in areas used for logging and recreational

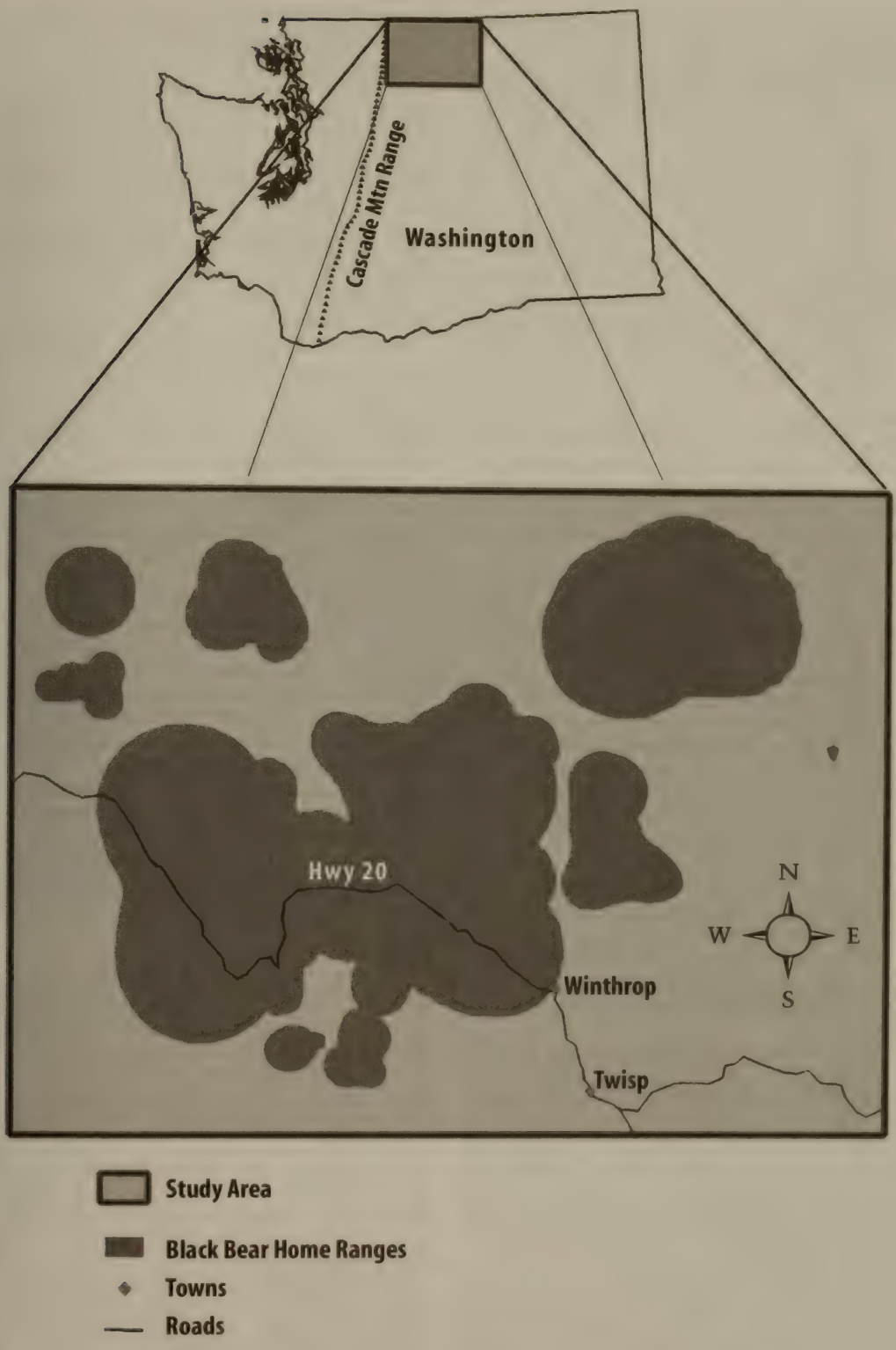


FIGURE 1. The Okanogan Study Area in the northeastern Cascades of Washington.

activities. Elevations range from about 500 m in the valley bottoms to 3000 m near the crest of the Cascade mountains. Precipitation near the Cascade crest averaged about 150-200 cm/year and precipitation at the lower elevations on the east side of the study area averaged 25-30 cm/year, falling mostly as snow. Vegetation conditions varied from open Bitterbrush *(Purshia tridentata)* slopes on the low elevation eastern portion of the study area, to Douglas-fir *(Pseudotsuga menziesii)* and Ponderosa Pine *(Pinus ponderosa)* forests at the lower and mid elevations, and montane and alpine vegetation beginning at about 1500 m. Roads are generally distributed along the drainages and along the eastern portion of the study area in the vicinity of human communities. Road densities range from <1 km/km^2 to a high of >3 km/km^2.

Methods

Black Bears were captured in Aldrich snares or darted from a helicopter and fitted with radio-collars and monitored 1-2 times/week using aerial telemetry from 1995 to 1998 (see Koehler et al. 2001 for details). This allowed bears to be tracked to their dens and entry and exit dates to be estimated.

Once bears were assumed to be denned, 2-3 additional telemetry flights were used to verify denning and the den location. Den locations were plotted on 1:24 000 United States Geological Survey quad maps and then digitized into an ARC INFO geographic information system (GIS). The accuracy of the aerial telemetry locations was evaluated with 54 test collars and found to be 180 meters (±63 meters, 95% CI). Because dens were located using multiple aerial relocations their accuracy is likely higher than the relocations based on single observations. The den locations were probably accurate to within 100 meters.

The vegetation map developed for the North Cascades using Landsat and ground sampling (Gaines et al. 1994) provided the basis for the development of Black Bear habitat maps. These vegetation data were updated to account for fires and timber harvest that have occurred since the original mapping was completed. A list of the vegetation types used in this analysis is shown in Table 1.

Digital terrain data were used to develop elevation zones and aspect categories (Table 1). The study area was divided into five elevation zones: 501-1000 meters, 1001-1500 meters, 1501-2000 meters, 2001-2500 meters, and >2500 meters. The study area was also classified into four aspect categories: North (271-45 degrees), East (46 to 135 degrees), South (136-225 degrees), and West (226-270 degrees). The location of each den site was digitized using the GIS to determine the appropriated elevation and aspect category.

The most current roads data layer (as of 1998) available on the Okanogan National Forest was used to assess roads in two ways. First, a moving windows GIS routine with a 1-km radius circular window was used to develop a road density map of the study area. Road densities were divided into the following categories: (1) areas with no open roads >200 ha in size, (2) areas with no open roads 40-200 ha in size, (3) areas with no open roads <40 ha in size, (4) areas with open road densities from 0.1-1 km/km^2, and (5) areas with open road densities > 1 km/km^2. Second, GIS maps were used to determine the straight-line distance from den sites and 200 random points within the study area to the nearest open road. These distances were recorded as continuous variables and then categorized into: 0-500, 501-1000, 1001-2000, 2001-3000, 3001-4000, 4001-5000, and >5000 meters.

All statistical analyses were conducted using PROSTAT (version 1.52) statistical software package. T-tests were used to determine if any statistical differences occurred between male and female den site locations for continuous variables (elevation, distance to roads). For categorical variables (road density zone, aspect, vegetation type), proportions of den sites in each category were arcsine transformed prior to testing for differences between males and females. Chi-Square and Kolmogorov-Smirnov (K-S) goodness of fit tests (Zar 1996) were used to determine if the den site characteristics differed from those available within the study area. K-S tests were used for variables that were recorded on an ordinal scale (Zar 1996) such as road densities, elevations, and distance from roads. The boundary of the study area encompassed all of the movements of the radio-collared bears during the study period and was delineated by major ridges and drainages (Alldredge et al. 1998). Analyses were conducted for all den sites, male den sites, and female den sites.

A GIS-based denning habitat model was developed using den site characteristics that were found to be significant when data for bear dens were pooled. This model was used to develop GIS maps of potential denning habitat within the study area. Summary statistics were derived from the potential denning habitat maps.

Results

Male Black Bears (n = 20) entered their dens (n = 21 entry dates) between 22 October and 19 November (Table 2). Females (n = 9) entered dens (n = 20 entry dates) from 15 October to 19 November (Table 2). For male Black Bears (n = 9) emergence dates (n = 16) ranged from 4 April to 7 May, and female (n = 7) emergence dates (n = 12) ranged from 9 April to 22 May (Table 2).

A total of 65 den sites were located between 1995 and 1998, representing den sites used by 29 different Black Bears. Twenty-nine den sites from nine different female Black Bears, and 36 den sites from 20 male bears were used in this analysis.

Males and females denned at similar distances to roads ($t = -0.024$, $p = 0.98$) and at similar elevations ($t = -1.103$, $p = 0.27$). Female Black Bear dens were located an average of 4339 meters (±2493 95% CI) from the nearest roads and at 1550 meters (±143 95%

TABLE 1. Den site variables and their availabity, and number of den sites used in the analysis of den site selection by Black Bears on the Okanogan Study Area, 1995-1998.

	% Available No.	Den Sites (%)
Vegetation Types		
Dry Forest (PIPO, PIPO/PSME)	18.0	9 (13.9)
Wet Forest (TSHE, ABAM)	2.0	1 (1.5)
High Elevation Forest (ABLA, PIEN, PICO, LALY, PIAL)	50.0	35 (53.9)
Deciduous Forest	3.0	1 (1.5)
Alpine/subalpine Meadow	16.0	9 (13.9)
Montane (non-forested shrub and herb dominated)	5.0	2 (3.0)
Low Elevation Shrub/Herb	3.0	6 (9.2)
Non-vegetated (Water, barren, snow, rock, unclassified)	3.0	2 (3.0)
Elevation Zones		
501-1000 meters	15.0	5 (7.6)
1001-1500 meters	31.2	16 (24.6)
1501-2000 meters	24.5	38 (58.5)
2001-2500 meters	28.9	6 (9.2)
>2500 meters	0.4	0
Aspect Categories		
North = 271-45 degrees	21.2	21 (32.3)
East = 46-135 degrees	27.9	17 (26.1)
South = 136-225 degrees	24.7	14 (21.5)
West = 226-270 degrees	25.0	13 (20.0)
Distance to Nearest Road Categories		
0-500 meters	35.5	15 (23.1)
501-1000 meters	9.0	4 (6.1)
1001-2000 meters	11.5	11 (16.9)
2001-3000 meters	7.5	10 (15.4)
3001-4000 meters	7.5	4 (6.1)
4001-5000 meters	4.0	6 (9.2)
>5000 meters	25.0	15 (23.1)
Road Density Zone		
Areas with no roads 0-40 ha in size.	0.1	0
Areas with no roads 41-200 ha in size.	14.1	0
Areas with no roads >200 ha in size.	65.9	53 (82.2)
Areas with road densities 0.1-1 km/km^2	5.9	5 (7.7)
Areas with road densities > 1 km/km^2	14.1	7 (10.8)

CI) in elevation. Male den sites were located an average of 4373 meters (±1579 95% CI) from the nearest road and at 1649 meters (±118 95% CI) in elevation. There were no differences between male and female den site locations for road density zones ($t = 0.025$, $p = 0.810$), aspect ($t = 0.001$, $p = 0.999$), and vegetation type ($t = 0.187$, $p = 0.857$). Based on the results of these analyses, no differences were identified between male and female den sites so I pooled den sites for the remainder of the analyses.

When compared to their availability within the study area, several habitat variables were correlated with den site selection. Black Bears used den sites with the following characteristics: areas with no open roads >200 ha in size (82% of the den sites, $d_{max} = 10$, $p < 0.05$), >500 meters from an open road (77% of the den sites, $d_{max} = 11$, $p = 0.02$), 1501-2000 meters in elevation (58% of the den sites, $d_{max} = 14$, $p = 0.002$). Aspect (Chi Square = 4.74, $p = 0.19$) and vegetation (Chi Square = 2.99, $p = 0.88$) were not used different than expected.

A GIS model of denning habitat within the study area was developed based on the following: areas with no open roads that were >200 ha in size, areas that were >500 meters from the nearest open road, and areas that were between 1500 to 2000 meters in elevation. These variables were used to produce a map of potential denning habitat using ARC INFO GIS for a large portion of the Okanogan National Forest (Figure 2). Approximately 276015 ha of potential denning habitat were identified, which included about 39% of the Okanogan National Forest lands west of the Okanogan River. Approximately 61% of the potential denning habitat is located within designated wilderness areas.

TABLE 2. A comparison of Black Bear denning entrance and emergence dates from studies conducted in the western United States and southwestern Canada.

Sex	Entrance Dates	Emergence Dates	Study Area Location	References
Male	2nd week October – 1st week November	2nd – 4th week April	NW Montana	Kasworm and Manley 1988
Female	1st-3rd week October	3rd week April – 2nd week May	NW Montana	Kasworm and Manley 1988
NA	9 October – 27 November	11-30 April	West-central Idaho	Amstrup and Beecham 1976
NA	late October – early November	mid-April – mid-May	N-central Montana	Jonkel and Cowan 1971
NA	13 October – 30 November	20 March – 5 May	NW Montana	Aune 1994
NA	mid-November – early December	early March – early May	Sierra/Sweetwater Moutains, California	Goodrich and Berger 1994
NA	end September – early November	early April – early May	N-central Montana	Mack 1989
NA	mid-October	mid-May	SW British Columbia	Allen 2001
Male	22 October – 19 November	4 April – 7 May	N-central Washington	This Study
Female	15 October – 19 November	9 April – 22 May	N-central Washington	This Study

Discussion

The den entrance dates from this study appeared to be earlier than those reported for the Sierra and Sweetwater Mountains of California and Nevada (Goodrich and Berger 1994), but were similar to the dates reported from northwestern Montana (Jonkel and Cowan 1971; Kasworm and Manley 1988; Aune 1994), southwestern British Columbia (Allen 2001), and west-central Idaho (Amstrup and Beecham 1976; Reynolds and Beecham 1980) (Table 2). The den emergence dates for Black Bears from this study were similar to those reported for northwestern Montana (Jonkel and Cowan 1971; Kasworm and Manley 1988; Aune 1994) and west-central Idaho (Amstrup and Beecham 1976; Reynolds and Beecham 1980) (Table 2). Black Bears in the Sierra and Sweetwater mountains of California and Nevada emerged from their dens earlier (Goodrich and Berger 1994) (Table 2).

A variety of factors have been described that appear to influence the denning period of Black Bears. Some researchers suggested that the fall food supply has the most important influence on den entrance (Tietje and Ruff 1980; Beecham et al. 1983; O'Pezio et al. 1983), and others suggested the importance of weather (Lindzey and Meslow 1976). It may be a combination of factors that vary by geographic location which ultimately determine Black Bear denning periods. My observations suggest that fall food supply and the availability of adequate snow cover for insulation are important factors that determine when bears enter dens in north-central Washington. Understanding the denning chronology of Black Bears should be useful to managers to coordinate human activities to reduce disturbance to denned bears (Mack 1989; Goodrich and Berger 1994).

Linnell et al. (2000) reviewed the available literature on the characteristics of Black Bear den sites and found that in more mountainous areas 20-50 degree slopes and moderate elevations were generally used. Aspect selection, however, was complex and generally presumed to be influenced by the local stability of snow conditions (Linnell et al. 2000). Research conducted in the western US also reported a wide variety of den site situations. For example Lindzey and Meslow (1976) reported that the percent slope or the aspect did not influence use of den sites by Black Bears on Long Island, Washington. Goodrich and Berger (1994) reported that Black Bears denning in the Sierra Mountains in California selected north to east-facing aspects and selected slopes over level areas for denning. Mack (1989) and LeCount (1983) reported that most dens in their study areas (north-central Montana and Arizona, respectively) occurred on northerly aspects. However, in the Sweetwater Mountains, California, bears used slopes or aspects for denning equal to their availability (Goodrich and Berger 1994). Slope and aspect were not significant variables in this study either, although more male den sites were located on north slopes than female den sites. Elevation was important to den site use by Black Bears in this study and in the Beartooth Mountains of Montana (Mack 1989). This may be a response by bears to move to the higher

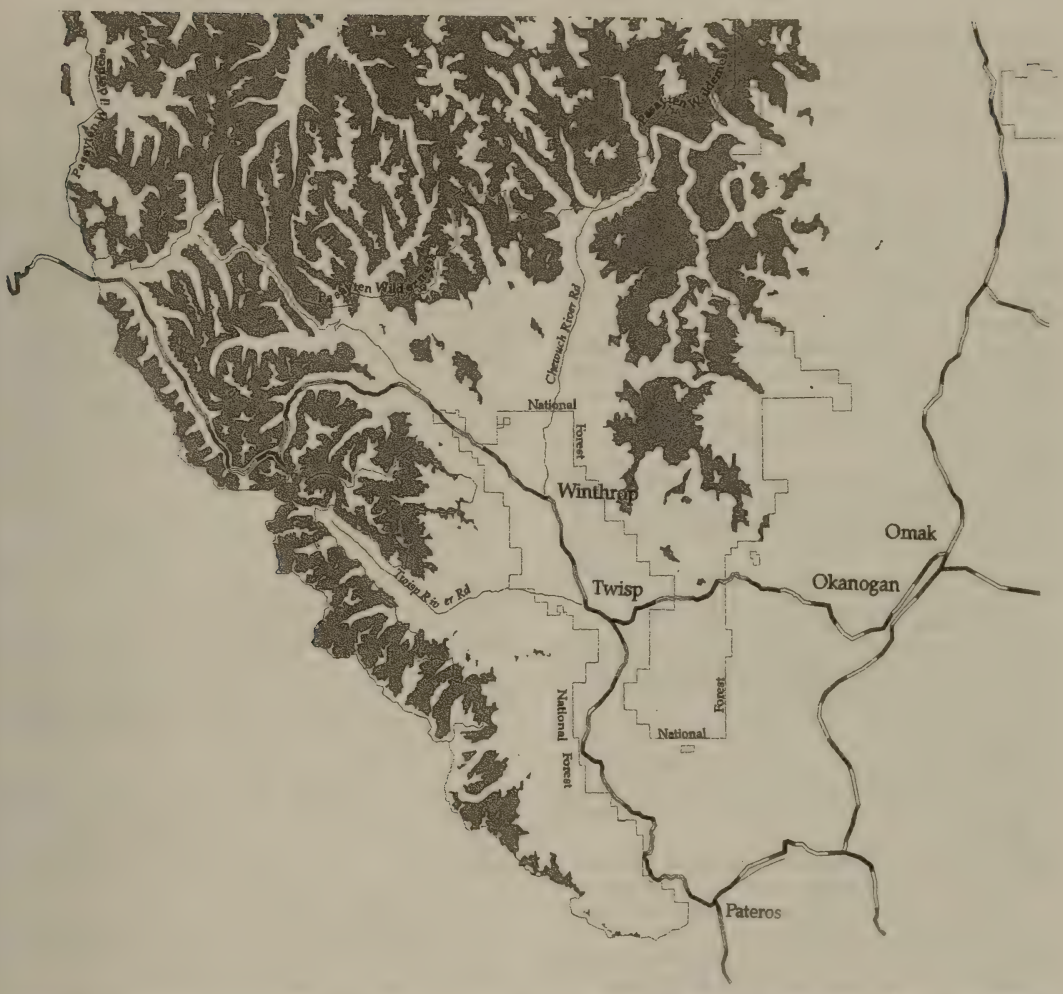


FIGURE 2. The distribution of potential denning habitat (shaded areas) based on the denning habitat model for the Okanogan National Forest, Washington.

elevations prior to denning where snow pack is greater resulting in better insulative qualities (Craighead and Craighead 1972).

Road aspects were correlated with den sites used by bears in this and other study areas. Goodrich and Berger (1994) reported that Black Bears generally denned at distances ≥0.8 km from roads and Tietje and Ruff (1983) reported distances of ≥0.3 km. These figures are comparable to the >0.5 km from dens to open roads from this study. Several authors have suggested that bears use den sites that are well concealed (Beecham et al. 1983; LeCount 1983) and inaccessible to humans (Novick and Stewart 1982; Goodrich and Berger 1994). This may be an important adaptive strategy to avoid predation (Paquet and Carbyn 1986; Ross et al. 1988; Smith and Follman 1993) and reduce the potential of human disturbance. Several studies have shown that bears may abandon their dens if disturbed by humans (Lindey and Meslow 1976; Hamilton and Marchinton 1980; LeCount 1983; Goodrich and Berger 1994). Den abandonment can have consequences to bears by increasing winter fat loss (Tietje and Ruff 1980) which could influence cub production and survival (Mack 1989). Rogers (1976) showed that if fat reserves drop too low, embryo implantation and fetal development may be halted. More research is needed to understand the physiological consequences of various levels and types of human activities (Linnell et al. 2000).

The potential denning habitat model, in combination with the information about the denning chronology of Black Bears in the study area should provide managers with tools to evaluate the affects of forest management activities on bear denning. In addition, this information could be used by managers to coordinate human activities to reduce the potential for disturbance to bears

during the denning period. This may be important as human activities have been shown to cause bears to abandon their dens (Goodrich and Berger 1994), and can lead to decreased survival and productivity (Johnson and Pelton 1981).

Acknowledgments

Funding for this project was provided by the Washington Department of Fish and Wildlife Black Bear Research Project and the U.S. Forest Service. I think Ken Raedeke, John Marzluff, Jim Agee, John Lehmkuhl, and Gary Koehler for their reviews of previous versions of this manuscript. I thank Andrea Gold, Ginger Holser, and Danielle Munzing for their field assistance.

Literature Cited

Alldredge, J. R., D. L. Thomas, and **L. L. McDonald.** 1998. Survey and comparison of methods for study of resource selection. Journal of Agricultural, Biological, and Environmental Statistics 3: 237-253.

Allen, M. 2001. [Abstract] Denning ecology of Black Bears in southwest British Columbia. Proceedings of the 7th Western Black Bear Workshop, Coos Bay, Oregon.

Alt, G. L. 1984. Black bear cub mortality due to flooding of natal dens. Journal of Wildlife Management 48: 1432-1434.

Amstrup, S. C., and **J. Beecham**. 1976. Activity patterns of radio-collared Black Bears in Idaho. Journal of Wildlife Management 40: 340-348.

Aune, K. E. 1994. Comparative ecology of black and grizzly bears on the Rocky Mountain front, Montana. International Conference on Bear Research and Management 9: 365-374.

Beecham, J. J., D. G. Reynolds, and **M. G. Hornocker**. 1983. Black bear denning activities and den characteristics in west-central Idaho. International Conference on Bear Research and Management 5: 79-86.

Boyd, D. K., and **E. E. Heger**. 2000. Predation of a denned Black Bear, *Ursus americanus*, by a grizzly bear, *Ursus arctos*. Canadian Field-Naturalist 114: 507-508.

Claar, J. J., N. Anderson, D. Boyd, M. Cherry, B. Conard, R. Hompesch, S. Miller, G. Ohlson, H. Ihisle Pac, J. Waller, T. Wittinger, and **H. Youmans**. 1999. Carnivores. Pages 7.10-7.63 *in* Effects of recreation on Rocky Mountain wildlife: A Review for Montana. *Coordinated by* G. Joslin and H. Youmans, Committee on Effects of Recreation on Wildlife. Montana Chapter of The Wildlife Society. 307 pages.

Clark, J. D., S. G. Hayes, and **J. M. Pledger**. 1998. A female Black Bear denning habitat model using a geographic information system. Ursus 10: 181-185.

Craighead, F. C., and **J. J. Craighead**. 1972. Grizzly bear prehibernation and denning activities as determined by radiotracking. Wildlife Monograph (32). 35 pages.

Ewer, R. F. 1973. The carnivores. Cornell University Press, Ithaca, New York. 494 pages.

Folk, F. E., M. A. Folk, and **J. J. Minor**. 1972. Physiological condition of three species of bears in winter dens. International Conference on Bear Research and Management 2: 107-124.

Gaines, W. L., R. H. Naney, P. H. Morrison, J. R. Eby, G. F. Wooten, and **J. A. Almack**. 1994. Use of Landsat multispectral scanner imagery and geographic information systems to map vegetation in the North Cascades ecosystem. International Conference on Bear Research and Management 9: 533-547.

Goodrich, J. M., and **J. Berger**. 1994. Winter recreation and hibernating Black Bears *Ursus americanus*. Biological Conservation 6: 105-110.

Hamilton, R. J., and **R. L. Marchinton**. 1980. Denning activity of Black Bears in the coastal plain of North Carolina. Proceedings of the 4th International Conference on Bear Research and Management, Kalispell, Montana.

Hellgren, E. C., and **M. R. Vaughan**. 1989. Denning ecology of Black Bears in a southeastern wetland. Journal of Wildlife Management 53: 347-353.

Hillman, L. L., and **D. L. Yow**. 1986. Timber management for Black Bear. Proceedings of the Eastern Workshop on Black Bear Management and Research 8: 125-136.

Johnson, K. G., D. O. Johnson, and **M. R. Pelton**. 1978. Simulation of winter heat loss for a Black Bear in a closed tree den. Proceedings of the Eastern Workshop on Black Bear Management and Research 4: 155-166.

Johnson, K. G., and **M. R. Pelton**. 1980. Environmental relationships and the denning period of Black Bears in Tennessee. Journal of Mammalogy 61: 653-660.

Johnson, K. G., and **M. R. Pelton**. 1981. Selection and availability of dens for black bears in Tennessee. Journal of Wildlife Management 45: 111-119.

Jonkel, C. J., and **I. M. Cowan**. 1971. The Black Bear in the spruce-fir forest. Wildlife Monograph (27). 57 pages.

Kasworm, W., and **T. Manley**. 1988. Grizzly bear and Black Bear ecology in the Cabinet Mountains of northwest Montana. Montana Department of Fish, Wildlife and Parks, Helena, Montana. 122 pages.

Koehler, G. M., P. Briggs Hall, M. H. Norton, and **D. J. Pierce.** 2001. Implant- versus Collar-transmitter use on Black Bears. Wildlife Society Bulletin 29: 600-605.

LeCount, A. L. 1983. Denning ecology of Black Bears in central Arizona. International Conference on Bear Research and Management 5: 71-78.

Lindzey, F. G., and **E. C. Meslow**. 1976. Winter dormancy in Black Bears in southwestern Washington. Journal of Wildlife Management 40: 408-415.

Linnell, J. D. C., J. E. Swenson, R. Andersen, and **B. Barnes**. 2000. How vulnerable are denning bear to disturbance. Wildlife Society Bulletin 28: 400-413.

Mack, J. A. 1989. Black bear dens in the Beartooth Face, south-central Montana. International Conference on Bear Research and Management 8: 273-277.

Nelson, R. A., H. W. Wahner, J. D. Jones, R. D. Ellefson, and **P. E. Zollman**. 1973. Metabolism of bears before, during and after winter sleep. American Journal of Physiology 224: 491-496.

Nelson, R. A., and **T. D. Beck**. 1984. Hibernation adaptation in the Black Bear: implication for management. Proceedings of the Eastern Workshop on Black Bear Research and Management 7: 48-53.

Novick, H. J., and **G. R. Stewart**. 1982. Home range and habitat preferences of black bears in the San Bernadino Mountains of southern California. California Fish and Game 67: 21-35.

Oli, M. K., J. A. Jacobson, and **B. D. Leopold**. 1997. Denning ecology of Black Bears in the White River National Wildlife Refuge, Arkansas. Journal of Wildlife Management 61: 700-706.

O'Pezio, J., S. H. Clarke, and **C. Hackford**. 1983. Chronology of Black Bear denning in the Catskill region of

New York. International Conference on Bear Research and Management 5: 87-94.

Paquet, P. C. and **L. N. Carbyn**. 1986. Wolves, *Canis lupus,* killing denning black bears, *Ursus americanus*, in the Riding Mountain National Park area. Canadian Field-Naturalist 100: 371-372.

Pelton, M. R., L. E. Beeman, and **D. C. Eager**. 1980. Den selection of Black Bears in the Great Smoky Mountains National Park. International Conference on Bear Research and Management 4: 149-152.

Pelton, M. R. 1985. Habitat needs of Black Bears in the east. Pages 49-53 *in* Wilderness and natural areas in eastern United States: A management challenge. *Edited by* D.L. Kulhavy and R. N. Conner. Stephen F. Austin University, Nacogdoches, Texas.

Poekler, R. J., and **H. D. Hartwell**. 1973. Black bear of Washington: its biology, natural history, and relationship to forest regeneration. Washington State Department of Game, Biology Bulletin (14), Olympia, Washington.

Reynolds, D., and **J. J. Beecham**. 1980. Home range activities and reproduction of Black Bears in west-central Idaho. International Conference on Bear Research and Management 3: 181-190.

Rogers, L. L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of Black Bears. Transactions of the North American Wildlife and Natural Resources Conference 41: 431-438.

Ross, P. I., G. E. Hornbeck, and **B. L. Horejsi**. 1988. Late denning Black Bear killed by grizzly bear. Journal of Mammalogy 69: 818-820.

Schooley, R. L., C. R. McLaughlin, G. J. Matula, Jr., and **W. B. Krohn**. 1994. Denning chronology of female Black Bears: effects of food, weather, and reproduction. Journal of Mammalogy 75: 466-477.

Smith, T. R. 1985. Ecology of Black Bears in the bottomland hardwood forest in Arkansas. Ph.D. thesis, University of Tennessee, Knoxville. 209 pages.

Smith, M. E., and **E. H. Follman**. 1993. Grizzly bear, *Ursus arctos*, predation of a denned Black Bear, *Ursus americanus*. Canadian Field-Naturalist 107: 97-99.

Tietje, W. D., and **R. L. Ruff**. 1980. Denning behavior of Black Bears in boreal forest in Alberta. Journal of Wildlife Management 44: 858-870.

Weaver, K. M., D. K. Tabberer, L. U. Moore, Jr., G. A. Chandler, J. C. Posey, and **M. R. Pelton.** 1990. Bottomland hardwood forest management for Black Bears in Louisiana. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 44: 342-350.

Weaver, K., and **M. R. Pelton**. 1994. Denning ecology of Black Bears in the Tensas River Basin of Louisiana. International Conference on Bear Research and Management 9: 427-433.

Wooding, J. D., and **T. S. Hardisky**. 1992. Black bear denning in northcentral Florida. Journal of Mammalogy 73: 895-898.

Zar, J. H. 1996. Biostatistical Analysis. 3rd Edition. Prentice Hall, Upper Saddle River, New Jersey.

Received 18 December 2002
Accepted 5 April 2004

First Report of a Sea Louse, *Lepeophtheirus salmonis,* Infestation on Juvenile Pink Salmon, *Oncorhynchus gorbuscha,* in Nearshore Habitat

ALEXANDRA B. MORTON[1] and ROB WILLIAMS[2]

[1] Raincoast Research, Simoom Sound, British Columbia, V0P 1S0 Canada; wildorca@island.net
[2] Sea Mammal Research Unit, Gatty Marine Lab, University of St Andrews, St Andrews, Fife, Scotland, KY16 8LB United Kingdom

Morton, Alexandra, and Rob Williams. 2003. First report of a Sea Louse, *Lepeophtheirus salmonis,* infestation on juvenile Pink Salmon, *Oncorhynchus gorbuscha,* in nearshore habitat. Canadian Field-Naturalist 117(4): 634-641.

High infestation rates of the Sea Louse (*Lepeophtheirus salmonis*) have been reported on juvenile salmonids in Europe since 1989; however, this species has not been reported on juvenile Pacific salmonids until now. Magnitude of Sea Lice infestation was examined in 2001 on juvenile Pink Salmon (*Oncorhynchus gorbuscha*) migrating through a British Columbia archipelago. On average, the 751 juvenile Pink Salmon sampled weighed 2.25 g (± 0.039 SE), were infected with 11.3 (± 0.41 SE) Sea Lice per fish and 6.1 (± 0.24SE) Sea Lice per gram host weight. Fully 75.0% of fish were infected at loads equivalent to or higher than the lethal limit reported for much larger Sea Trout (*Salmo trutta*) post-smolts. Abundance (Kruskal-Wallis statistic = 100.95, $p<0.0001$) and intensity (KW = 70.05, $p<0.0001$) of lice, and mean number of lice/g host weight (K-W = 112.23, $p<0.0001$) were significantly higher in juvenile Pink Salmon in close proximity to salmon farms, than in Pink Salmon distant from salmon farms.

Key Words: Pink Salmon, *Oncorhynchus gorbuscha*, Sea Lice, *Lepeophtheirus salmonis*, British Columbia, aquaculture, salmon farm.

The Sea Louse, *Lepeophtheirus salmonis,* is a common caligid parasite of salmonids throughout the Northern Hemisphere (Kabata 1973, 1979). Low natural abundance and minimal host damage characterise this species (Boxshall 1974; Wootten et al. 1982; Berland 1993; Nagasawa 1987). Epizootics of *L. salmonis* on wild salmonids were rare worldwide (White 1940; Wootten et al.1982; Nagasawa 1987) until 1989, when a series of outbreaks coincident with the presence of salmon farms occurred off the coasts of Ireland (Tully et al. 1993) and Norway (Birkeland 1996).

There has never been an outbreak of *L. salmonis* reported on juvenile Pacific salmon (*Oncorhynchus* sp.). The only record of an epizootic outbreak of this species on Pacific salmon occurred on adult Sockeye Salmon (*Oncorhynchus nerka*) holding at the head of an inlet (where salmon farms existed) due to low freshwater levels (Johnson et al. 1996). Conversely, Parker and Margolis (1964) did report an infestation of the generalist, non-salmonid-specific species, *Caligus clemensi,* on juvenile Pink Salmon (*Oncorhynchus gorbuscha),* which caused fin erosion.

The life cycle of *L. salmonis* has five phases and 10 stages (Kabata 1972; Johnson and Albright 1991a). Consequently, the approximate age of Sea Lice can be determined from first attachment until adulthood. The interval from hatching to infective capability (copepodid stage) is approximately 4 d at 10°C and 2 d at 15°C (Johnson and Albright 1991b); therefore host attachment is more likely to occur near the site of larval release (Tully et al. 1993). On adult wild salmon, Sea Lice populations are predominantly adult phase (Pike and Wadsworth 1999); while predominantly juvenile infections are typical of infestations on wild salmonids in salmon-farmed areas (Tully et al. 1993; Bjørn and Finstad 2002).

Once attached, *L. salmonis* enters the first of four stationary chalimus stages. Next it develops into a preadult, where body shape changes into a smaller version of the final form and the louse becomes mobile (Johnson and Albright 1991a). A sudden increase in pathogenicity and host damage occurs when lice mature to the mobile, preadult stage (Grimnes and Jakobsen 1996; Bjørn and Finstad 1997). Grimnes and Jakobsen (1996) and Bjørn and Finstad (1997) reported that 0.75 -1.6 lice/g host weight was lethal to post-smolt Sea Trout (*Salmo trutta*). *Lepeophtheirus salmonis* is intolerant of fresh water (Schram et al. 1998; Hahnenkamp and Fyhn 1985; McLean et al.1990; Johnson and Albright 1991b). When transported upriver on maturing adult salmon, this generation of lice dies, thereby reducing inshore Sea Lice populations.

Virtually all research on *L. salmonis* pertains to Sea Trout, Atlantic Salmon (*Salmo salar*) and Arctic Charr (*Salvelinus alpinus*); however, Pink Salmon have a markedly different life cycle than these species. Pink Salmon have a fixed two-year life span (Heard 1991) and enter the marine environment in spring (March – May) at approximately 3.5 cm fork length (Heard 1991) and 0.24 g (Bailey et al. 1975). Pink Salmon thus enter seawater four to five times shorter than Atlantic salmon (Scott and Crossman 1973) and with a much lower mass. Atlantic Salmon enter seawater at approximately 30 g (Poole et al. 2003). Pink Salmon disperse rapidly from estuarine environments (Pearcy 1992), forming dense surface schools (Parker 1965) in the top few centimetres of the water column (Healey 1980). They exhibit strong shoreward orientation (Healey 1967,

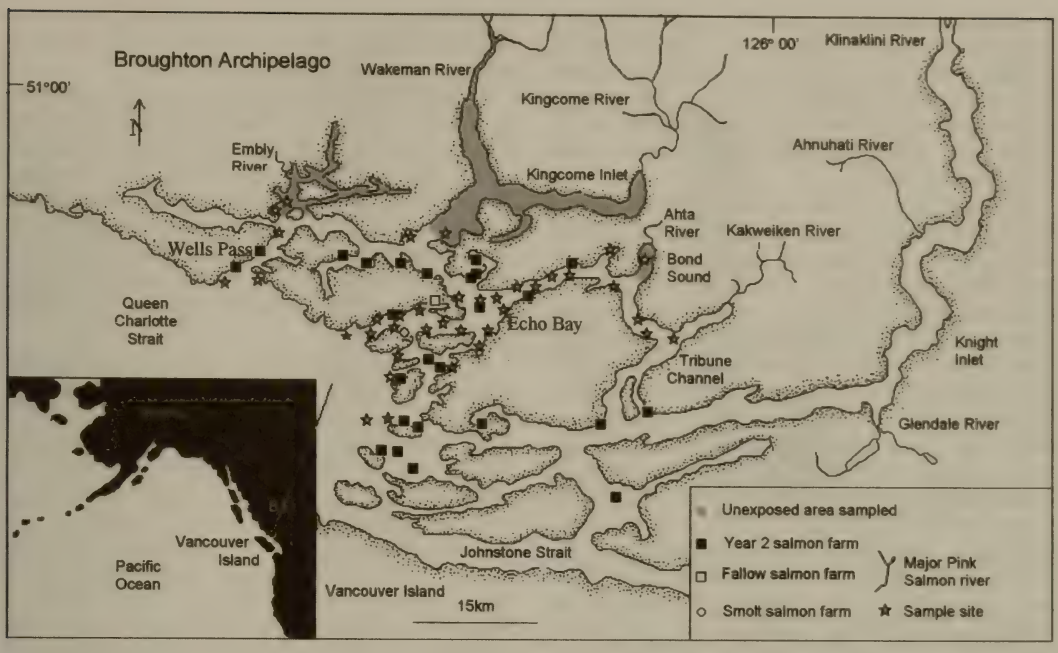


FIGURE 1. Map of the Broughton Archipelago, British Columbia, study area showing the eight major Pink Salmon-producing rivers, location of salmon farms and general areas where one or more sampling sites were located.

1980) and remain nearshore until they grow to approximately 6.0-7.0 cm fork length (Cooney et al. 1978*). Once reaching a length of 6.0-7.0 cm, Pink Salmon move offshore (LeBrasseur and Parker 1964; Cooney et al. 1978*). This transition, accompanied by a shift to lower lipid levels (Parker and Vanstone 1966), is considered "smolting" in Pink Salmon. Hereafter, Pink Salmon fry and smolts will be referred to collectively as juveniles.

In early June 2001, a local fisherman delivered a 5 cm juvenile Pink Salmon to us that was heavily infested with *L. salmonis*. Our response was this preliminary survey of juvenile Pink Salmon throughout the Broughton Archipelago to document the occurrence of this unusual infection. Here we report the results of a spontaneously organized survey of seaward-migrating Pink Salmon juveniles in the marine nearshore habitat of the Broughton Archipelago.

Methods

This study was conducted in the Broughton Archipelago, a ca. 400 km^2 network with 90 km of narrow passages and 200 km of inlets flushed by a 3.6 m mean tidal exchange. The Broughton Archipelago is a major natural production area for all native Pacific salmon species (*Oncorhynchus* sp.), except Sockeye. The eight major Pink Salmon rivers in the Broughton Archipelago collectively produce the fish referred to by Fisheries and Oceans Canada as the Area 12 Mainland Pink stock. This stock is a highly productive portion of even-year cycle Pink Salmon in southern British Columbia. Adult Pink Salmon returns to these eight rivers during 2000 totalled 3.6 million and over one-half of all Pink Salmon spawning escapement in southern British Columbia (PFRCC 2002*).

There were 26 Atlantic Salmon farm sites located in the Broughton Archipelago in 2001 (Figure 1). Sea Lice infestation of wild salmonids has occurred at some interval following major salmon farming activity in most salmon farmed areas (Anonymous 1997*). Epizootics on wild salmonids are often concurrent with Sea Lice outbreaks on farmed fish (Mackinnon 1997) and the effect of Sea Lice on wild salmonids in the vicinity of salmon farms seems particularly acute within long fjord/inlet-type environments (Holst et al. 2002*). Contrary to reporting requirements in other countries, the number of Sea Lice on farm salmon is not available in British Columbia.

Juvenile Pink Salmon were collected from schools spotted along the shoreline, using a 45 cm diameter dip net, fit with 5 mm knotless mesh on a 2.45 m pole, from a shallow draft 7.5 m boat (as per Bailey et al. 1975). This gear-type had the advantage of being available for a quick response to the observed infestation and allowed access and capture of juvenile Pink Salmon in the shallow waters where this species is found during its most juvenile life-stages. A dip net could have introduced bias by selecting for weaker, more heavily infested fish; however, while some bias can be assumed with any gear type, it remained constant

over time and among all exposure categories. Sampling took place between 12 June and 16 August 2001 at 46 sites, which were selected to provide reasonable geographic coverage of the study area, and to intercept all potential salmon migrating out from rivers in Knight Inlet, Kingcome Inlet, Tribune Channel and Wells Pass (Figure 1).

Reports of epizootics of *L. salmonis* on wild juvenile Atlantic salmonids (Sea Trout and Atlantic Salmon) specifically near fish farms (Tully et al. 1993; Birkeland 1996) prompted us to classify our sample sites post-hoc into three categories – *unexposed* (3-5.5 km "upstream" from all salmon farms, relative to direction of the juvenile salmon migration – 5 sites); *exposed* (within 60 m of Year 2 Atlantic Salmon pens, or where fish could only have swum past pens – 38 sites); and *smolt* (near a Year 1 farm where Atlantic Salmon had been in the saltwater for less than 6 months – 3 sites). Unexposed sites were comparable (e.g., not brackish) to exposed and smolt sites except for proximity to farms. The samples were collected in such a way as to provide good spatial coverage of the study area (Figure 1), in order to assess whether the infestation was restricted to the one fish presented to us. Our subsequent classification, to test whether variation in lice infestation could be explained partly due to proximity to fish farms, created an unbalanced sampling design for this aspect of the pilot study. This imbalance in number of sites between categories occurred for two reasons. Most of the Broughton Archipelago falls into the *exposed* category due to the high density of farms in the region. Secondly, this spontaneous survey was initiated after the juvenile Pink Salmon migration was well underway, with very few fish remaining in the more eastern, *unexposed* regions closer to the rivers. Collection sites were dispersed through the archipelago to include migration routes from all eight major Pink Salmon-producing rivers (Embly, Wakeman, Kingcome, Ahta, Kakweikan, Glendale, Ahnuhati and Klinaklini) (Figure 1), the waters adjacent to 21 Atlantic salmon farm sites and the seaward edge of the archipelago at Queen Charlotte Strait.

Each salmon was placed in a Whirl-pak™ specimen bag, and put on ice. Fish were weighed and measured (fork length). The species, number and age class of lice (using Johnson and Albright 1991a) were recorded using a 30× stereoscope after Bjørn and Finstad (1998). Specimens of the non-salmon-specific Sea Louse, *Caligus clemensi*, were distinguished from *L. salmonis* using the taxonomic key provided by Kabata (1972), counted, but were rare and not used in the analyses presented here.

We compared prevalence (percentage of fish with Sea Lice, *L. salmonis*), abundance (louse count per fish), and intensity (louse count per infected fish) (Margolis et al. 1982) among exposure categories. Box plots were produced in S-Plus 2000 (Release 3, MathSoft Inc.) to contrast the variation in lice counts (per fish and per gram host mass) with respect to exposure category. If any Kruskal-Wallis (K-W) test showed that the response differed among exposure category at the p=0.05 level, then Dunn's post-test was conducted to determine which pairs of exposure categories differed (Zar 1996).

Results

We sampled 751 juvenile Pink Salmon in waters that averaged 12.1 °C (±0.066SE), collecting mass, and length and Sea Lice counts. Overall, on average the fish hosted 11.3 (± 0.41SE) Sea Lice per fish and 6.1 (± 0.24SE) lice per gram host weight. Mean length was 5.9 cm (±0.034SE; range 2.8 to 10.4 cm) and mass was 2.3 g (±0.039SE; range 0.21 to 10.78 g) (Table 1). Fully 75.0% were infected at loads equivalent to or higher than 1.6 Sea Lice per gram of host mass.

We counted 8206 *L. salmonis*, with counts per fish ranging from 0 to 69. The most juvenile (copepodid

TABLE 1. Abundance, intensity, length and mass were compared using Kruskal-Wallis tests (the non-parametric equivalent of a one-way ANOVA). Results of Dunn's post-tests (Zar, 1996) for pairwise comparisons are given in the text.

	Exposed to Year-two salmon farm	Exposed to Year-one smolt farm	Unexposed to farms	K-W test (p-value)
prevalence (%)	98.4	90.6	68.4	
Abundance	12.3	4.2	1.9	100.95 (<0.0001)
(SE)	(0.45)	(0.61)	(0.33)	
Intensity	12.5	5.2	2.7	70.05 (<0.0001)
(SE)	(0.45)	(0.65)	(0.38)	
% of fish with ≥ 1.6 lice/g body weight	81.2	39.6	15.7	
mean length (cm)	5.9	6.2	6.4	14.89 (0.0006)
(SE)	(0.036)	(0.13)	(0.15)	
mean mass (g)	2.2	2.7	2.9	40.683 (<0.0001)
(SE)	(0.041)	(0.13)	(0.17)	
n (fish)	660	53	38	–

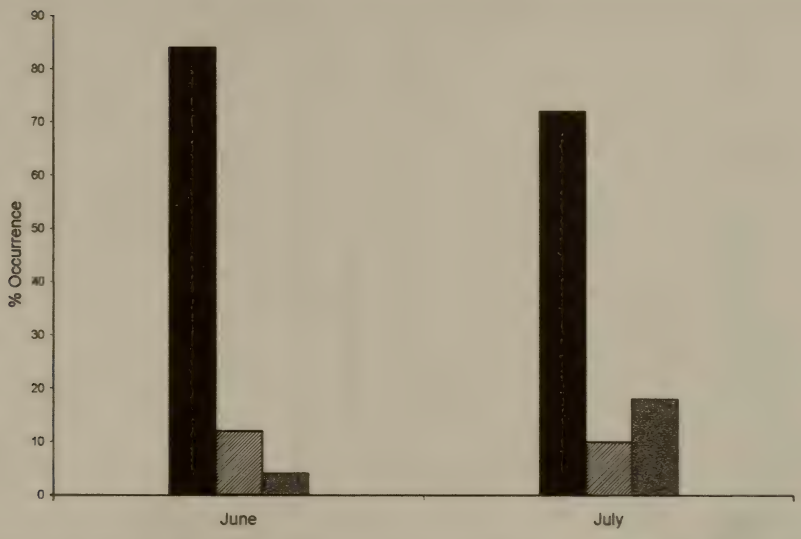


FIGURE 2. The percent occurrence of copepodid/chalimus lice (black), pre-adult (diagonal lines), and adult (spotted) per month.

and chalimus I-IV) stages dominated the lice population throughout June and July. These were only nine samples from August and so were not included (Figure 2). Adult lice were observed beginning on Day 21 of our study.

Lice burdens varied significantly among exposure categories (Table 1, Figure 3). Variation in median louse abundance was greater among the three exposure categories than would be expected by chance (Kruskal-Wallis (KW) test statistic 100.95; $p<0.0001$). Dunn's post-tests indicated that all three pairwise comparisons showed significant differences. Louse abundance on juvenile Pink Salmon sampled near farms holding adult Atlantic Salmon was significantly higher than that seen on fish sampled at unexposed sites (Mean Rank Difference (MRD) 183.5; $p<0.001$) or at farm sites holding Atlantic Salmon smolts (MRD 306.06; $p<0.001$). Fish from smolt-only sites had significantly higher louse abundance than fish from unexposed sites (MRD 122.47; $p<0.05$).

Of infected fish, median louse intensity varied more among exposure categories than one would expect by chance (KW 70.05; $p<0.0001$). Dunn's post-tests indicated that intensity was higher in fish sampled near farms containing adult Atlantic Salmon than in fish sampled near smolt-only sites (MRD 172.68; $p<0.001$) or unexposed sites (MRD 272.9; $p<0.001$). However, the difference in intensity between fish sampled near smolt-only and unexposed sites was not significantly different (MRD 100.22; $p>0.05$).

The number of lice per gram host weight (another response variable commonly used to report the magnitude of Sea Louse infestation) varied significantly among exposure categories (Figure 3; KW 112.23, $p<0.0001$). The median value of 4.7 lice per gram host mass of fish sampled near farms housing adult Atlantic Salmon was significantly higher than that of fish sampled near smolt farms (median 1.3 lice per gram host mass; MRD 203.59, $p<0.001$) and unexposed sites (median 0.6 lice per gram host mass; (MRD 315.18, $p<0.001$). Median values of smolt-only and unexposed samples were significantly different from one another ((MRD 111.59, $p<0.05$).

The size of juvenile Pink Salmon also varied among exposure categories (Table 1). Median length of juvenile Pink Salmon showed higher variation among exposure categories than one would expect by chance (KW 14.89; $p=0.0006$). Fish exposed to farms housing adult Atlantic Salmon were shorter than fish sampled at unexposed sites (MRD -119.28; $p<0.01$), but they were not significantly shorter than fish sampled near smolt farms (MRD -67.446; $p>0.05$). Smolt-only samples did not differ significantly in length than those sampled at unexposed sites (MRD -51.836; $p>0.05$). Variation in median mass of fish also showed higher variation among exposure categories than one would predict by chance (KW 40.683; $p<0.0001$). Fish sampled near adult Atlantic Salmon farms weighed significantly less than either fish sampled near smolt sites (MRD -131.18; $p<0.001$) or unexposed sites (MRD -181.99; $p<0.001$). No significant difference was found in mass of fish sampled near smolt farms or unexposed sites (MRD -50.809; $p>0.05$). The mass of salmon carrying <1.6 lice/g (mean 3.1 g ± 0.10SE; median 2.7 g; range 0.82 to 10.78 g) was significantly higher than that of salmon carrying ≥1.6 lice/g host mass (mean 2.0g ± 0.031SE; median 1.89 g; range 0.21 to 7.38 g) (Mann-Whitney U-statistic = 25004, $p<0.0001$). This effect is confounded by the non-identical distribution of fish lengths in the two samples; however, fish

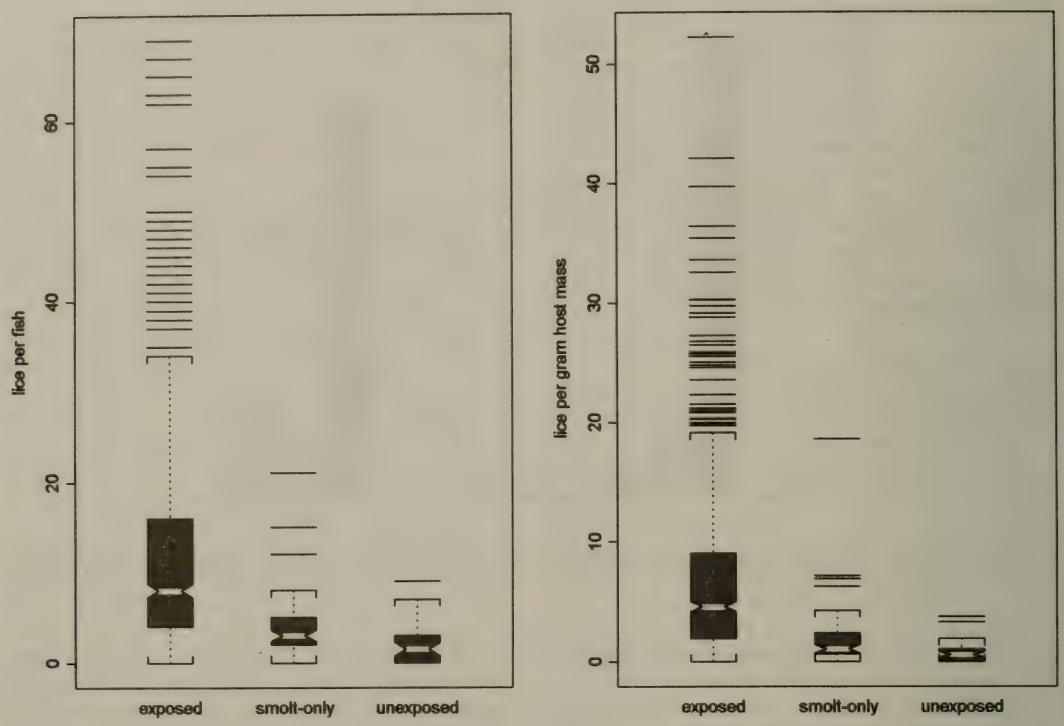


FIGURE 3. Boxplots showing range of lice abundance (left) and number of lice/g host weight (right) by exposure category. The line at the notch represents the median. Whiskers are drawn to 1.5 × (Inter-Quartile Range). Values beyond this are identified individually by horizontal lines. The skew indicated by these boxplots shows the need for non-parametric analyses.

carrying ≥1.6 lice per gram host mass weighed less, on average, than fish of the same length that carried less than 1.6 lice per gram host mass (Figure 4).

Discussion

This is the first report of *L. salmonis* infection on juvenile Pink Salmon. Our data suggest the infection was related to the presence of net-pen salmon farms in the immediate area (Table 1, Figure 3). The rate of infestation almost certainly reduced survivorship of the infected fish by compromising growth (Figure 4). The large percentage of infected fish raises concern for the health of the stock (Table 1).

Most research on *L. salmonis* infestation of juvenile wild salmonids pertains to Sea Trout, Atlantic Salmon and Arctic Charr. Finstad et al. (2000) estimated that juveniles of these species can tolerate up to 10 Sea Lice per fish. Observations on 3000 post-smolt Atlantic Salmon, in open oceanic waters from 1991 to present, did not find a single fish with more than 10 adult lice (Holst et al. 1992*). Among these, fish with close to 10 lice were physiologically compromised (reduced growth and low hematocrit values) (Holst, personal communication).

While wild Atlantic salmonids spend a year or more in fresh-water and the Atlantic Salmon, for example, enters sea water at approximately 30 g (Poole et al. 2003), Pink Salmon go to sea at approximately 0.24 g (Bailey et al. 1975). Given that experimental results show that young salmonids can tolerate approximately one louse per gram of body weight (Grimnes and Jakobsen 1996; Bjørn and Finstad 1997), it is reasonable to conclude that Pink Salmon of the weights we recorded were imperilled by the lice loads we report here (Figure 3). Note that this study took place well after the peak months of saltwater entry (Heard 1991). On average, the Pink Salmon we sampled were an order of magnitude heavier than the reported mass at which Pink Salmon leave fresh water. If the lice we report were present when the fish first entered the marine environment, the number of lice per gram host weight would have been proportionally larger. Thus, the figures we present may be underestimates of the magnitude of the infestation. Pink Salmon fry are subject to such heavy predation by yearling Coho when the Pink Salmon first put to sea that their margin of survival at this life-phase is considered slight and achieved only through rapid growth (Parker and LeBrasseur 1974). Thus any impact reducing growth could be considered adverse.

Local fishermen also brought in three infected Chum (*O. keta*) smolts (average, 51 Sea Lice/g), three in-

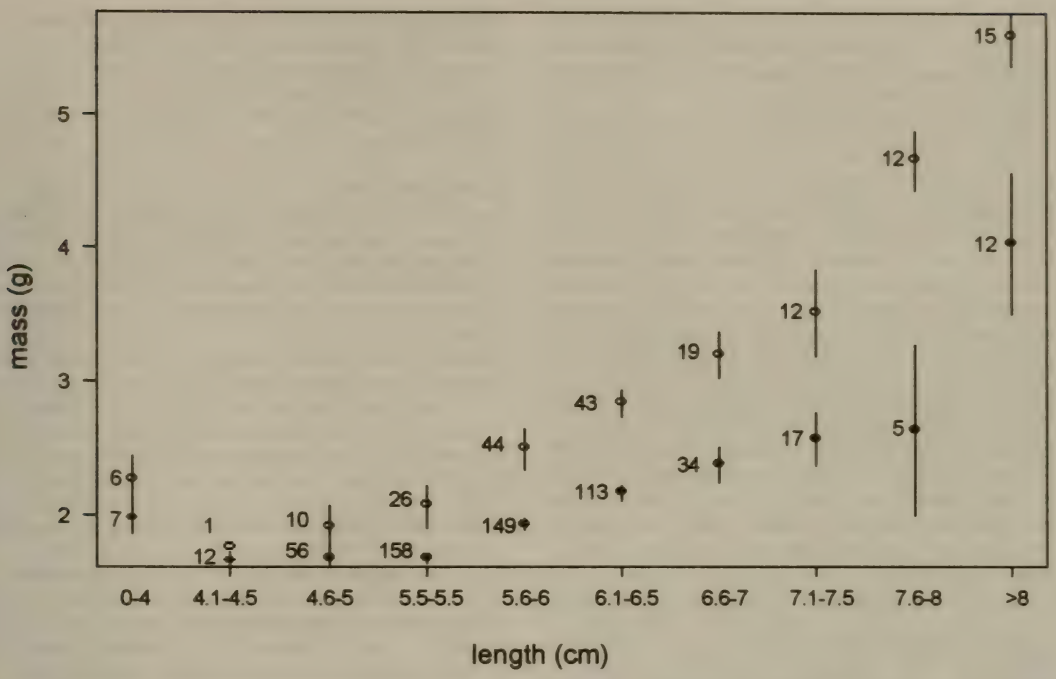


FIGURE 4. Scatterplot showing masses of fish of varying lengths. Empty circles represent fish with <1.6 lice per gram host mass, and filled circles represent fish with ≥1.6 lice per gram host mass, with standard error bars superimposed. The numbers to the left of the data points indicate the number of fish in each sample.

fected Coho (*O. kisutch*) (average, 24 Sea Lice/g) and two Chinook (*O. tshawytscha*) Salmon smolts (average, 29 Sea Lice/g), suggesting that this infestation was not limited to Pink Salmon. Unfortunately, our collection permit restricted species and gear-type, therefore we were unable to collect additional samples to quantify the extent of infestation among other salmonid species. However, this anecdotal evidence indicates that Sea Lice also were infecting other ecologically and economically important salmon species.

As we counted the Sea Lice, we noted extensive damage to the skin of the host juvenile Pink Salmon. Common marks included paired, pin-prick perforations through the skin. There were areas where the skin was removed and chalimus-stage lice affixed to the exposed flesh. Black spots were visible corresponding to reports of darkened localized cellular response of accumulated melanocytes (Pike and Wadsworth 1999). Bleeding at the base of the fins was observed frequently.

We infer that the source of the Sea Lice must have been located within the Broughton Archipelago for several reasons. First, the fish sampled were moving generally west, from rivers deep within the archipelago's inland reaches (Figure 1) and thus were unlikely to have been exposed to larval lice beyond the archipelago. Secondly, such young salmon, averaging 5.9 cm and 2.25 g, but some with yolk sacs still visible, would seem unlikely to have migrated from outside the 400 km^2 study area. Finally, Sea Lice infestations that are dominated by the short-lived juvenile life-history stages have been shown to be indicative of a local source of gravid female lice (Costelloe et al. 1996). Throughout this study, 78% of the lice we sampled were juveniles (copepodid and chalimus), which endure only a matter of days (Johnson and Albright 1991b) (Figure 2). Thus, gravid female Sea Lice had to be present locally and continuously. Since *Lepeophtheirus salmonis* is salmon–specific this can only mean a large, host population of salmon existed in the Broughton throughout this study. No large wild salmon population could be identified in the study area during this time period (Neidrauer, personal communication). While there are no reports made public on the number of farm salmon in the Broughton Archipelago, there were 26 salmon farms, some with over one million stationary Atlantic Salmon per farm (Nayler et al.).

The inability of *L. salmonis* to tolerate freshwater suggests that a mechanism has evolved whereby young salmon do not encounter this parasite until farther offshore, when they have attained a more robust body size than that observed in this study. If the Broughton Archipelago is now providing over-wintering habitat for Sea Lice in its nearshore environment, then the efficacy of that natural safety mechanism is compromised. In 2002, when the juvenile salmon examined in this study matured, 98% failed to return to the rivers

to spawn (PFRCC 2002*). This Area 12 Mainland Pink Salmon stock collapsed amidst good to excellent Pink Salmon returns elsewhere coast-wide throughout British Columbia (PFRCC 2002*).

While the cause of this crash has not been identified with certainty, the PFRCC (2002*) could not find any fresh water or open-ocean factors that could have affected all of the Broughton Archipelago Pink Salmon runs, and indeed, only the Broughton Archipelago Pink Salmon runs. The available evidence pointed to factors confined to the Broughton Archipelago's nearshore marine environment (PFRCC 2002*). This nearshore environment is both critical Pink Salmon rearing habitat and heavily used by the salmon farming industry. Clearly, identifying the source of the Lice with greater certainty requires additional experimental research. A preliminary step would be to require farmers to report the number of Sea Lice on farm salmon, as farmers in other countries are required to do. However, given that damaging Sea Lice outbreaks have occurred on juvenile wild salmon in many places where salmon farms exist, it would seem reasonable to consider precautionary management of the primary suspect source of the infection, the gravid female lice on farm salmon. Such action might avert potentially irreversible harm to the Area 12 Mainland Pink Salmon stock as science and policy mature to manage this young industry in British Columbia.

Acknowledgments

We thank Jens Christian Holst, Institute of Marine Research (Bergen, Norway), Bill Heard and Alan Walker for their contributions, and Simon Northridge, Sascha Hooker, and several colleagues and three anonymous reviewers who improved earlier drafts of this paper. Thank you also to Glen Neidrauer, (Fisheries and Oceans Canada patrolman, Simoom Sound, BC V0P 1S0) for answering our questions regarding presence of wild salmon stocks. This work was in part supported by Tides Canada. RW was supported by the Jane Marcher Foundation. Collection permit MMM 2001-MMM 2002 was granted to this project.

Documents Cited (marked * in text)

Anonymous. 1997. Report of the workshop on the interactions between salmon lice and salmonids. Edinburgh, UK, 11-15 November 1996: ICES CM 1997/M: 4. Ref.; F. 204 pages.

Cooney, R. T., D. Urquhart, R. Nevé, J. Hilsinger, R. Clasby, and **D. Barnard**. 1978. Some aspects of the carrying capacity of Prince William Sound, Alaska for hatchery released pink and chum salmon fry. Alaska Sea Grant Report. 78-4; University of Alaska Institute of Marine Resources IMS R78-3:98 pages.

Holst, J. C., P. Jakobsen, F. Nilsen, M. Holm, L. Asplin, and **J. Aure**. 2002. Mortality of seaward migrating post smolts of Atlantic salmon due to salmon lice infection in western Norwegian salmon stocks. Atlantic Salmon Federation symposium Salmon on the Edge, Edinburgh July 15-18 (http://www.asf.ca/symposium2002/abstracts/3-1-noresea lice.html).

PFRCC (Pacific Fisheries Resource Conservation Council) 2002. 2002 Advisory: The protection of Broughton Archipelago Pink Salmon stocks. Appendix 1, Annex 2. Report to Minister of Fisheries and Oceans, and British Columbia Minister of Agriculture, Food and Fisheries, www.fish.bc.ca. 91 pages.

Literature Cited

Bailey, J. E., B. L. Wing, and **C. R. Mattson**. 1975. Zooplankton abundance and feeding habits of fry of Pink Salmon, *Oncorhynchus gorbuscha,* and Chum Salmon, *Oncorhynchus keta,* in Traitors Cove, Alaska, with speculations on the carrying capacity of the area. Fisheries Bulletin U.S. 73: 846-861.

Berland, B. 1993. Salmon lice on wild salmon (*Salmo salar* L.) in western Norway. Pages 179-187 *in* Pathogens of wild and farmed fish: Sea Lice. *Edited by* G. A. Boxshall and D. Defaye. Ellis Horwood, London. 378 pages.

Birkeland, K. 1996. Consequences of premature return by Sea Trout (*Salmo trutta*) infested with the salmon louse (*Lepeophtheirus salmonis* Krøyer); migration, growth and mortality. Canadian Journal of Fisheries and Aquatic Science 53: 2808-2813.

Bjørn, P. A., and **B. Finstad**.1997. The physiological effects of salmon lice infection on Sea Trout post-smolts. Nordic Journal of Freshwater Research 73: 60-72.

Bjørn, P. A., and **B. Finstad**. 1998. The development of salmon lice (*Lepeophtheirus salmonis*) on artificially infected Sea Trout (*Salmo trutta*) post smolts. Canadian Journal of Zoology 76: 970-977.

Bjørn, P. A., and **B. Finstad**. 2002. Salmon lice, *Lepeophtheirus salmonis*, (Krøyer), infestation in sympatric populations of Arctic char, *Salvelinus alpinus* (L.) and sea trout, *Salmo trutta* (L.), in areas near and distant from salmon farms. ICES Journal of Marine Science 59: 1-9.

Boxshall, G. A. 1974. Infections with parasitic copepods in North Sea marine fishes. Journal of Marine Biology Association U.K. 54: 355-372.

Costelloe, M., J. Costelloe, and **N. Roche**. 1996. Planktonic dispersion of larval salmon-lice, *Lepeophtheirus salmonis* associated with cultured salmon, *Salmo salar*, on the west coast of Ireland. Journal of Marine Biology Association U.K. 76: 141-149.

Grimnes, A., and **P. J. Jakobsen**.1966. The physiological effects of salmon lice infection on post-smolt of Atlantic salmon. Journal of Fisheries Biology 48: 1179-1194.

Hahnenkamp, L., and **H. J. Fyhn**.1985. The osmotic response of salmon louse, *Lepeophtheirus salmonis* (Copepoda: Caligidae), during the transition from sea water to fresh water. Journal of Comparative Physiology B 155: 357-365.

Healey, M. C. 1967. Orientation of Pink Salmon (*Oncorhynchus gorbuscha*) during early marine migration from Bella Coola River system. Journal of the Fisheries Research Board of Canada 24: 2321-2338.

Healey, M. C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. Pages 203-229 *in* Salmonid ecosystems of the North Pacific. *Edited by* W. J. McNeil and D. C. Himsworth. Oregon State University Press, Corvallis, OR.

Heard, W. 1991. Life history of Pink Salmon. Pages 121-230 *in* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. University of British Columbia Press. 564 pages.

Johnson, S. C., and **L. J. Albright.** 1991a. The development stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae). Canadian Journal of Zoology 69: 929-950.

Johnson, S. C., and **L. J. Albright.** 1991b. Development, growth and survival of *Lepeophtheirus salmonis* (Copepoda: Caligidae) under laboratory conditions. Journal of Marine Biology Association U.K. 71: 425-436.

Johnson, S. C., R. B. Blaylock, J. Elphick, and **K. D. Hyatt.** 1996. Disease induced by the sea louse *(Lepeophtheirus salmonis)* (Copepoda: Caligidae) in wild sockeye salmon (*Oncorhynchus nerka*) stocks of Alberni Inlet British Columbia. Canadian Journal of Fisheries and Aquatic Science 53: 2888-2897.

Kabata, Z.1972. Developmental stages of *Caligus clemensi* (Copepoda: Caligidae). Journal of the Fisheries Research Board of Canada 29: 1571-1593.

Kabata, Z. 1973. The species of *Lepeophtheirus salmonis* (Copepoda: Caligidae) from fish of British Columbia. Journal of the Fisheries Research Board of Canada 30: 729-759.

Kabata, Z. 1979. Parasitic copepoda of British Fishes. London, Ray Society. 468 pages.

LeBrasseur, R. J., and **R. R. Parker**. 1964. Growth rate of central British Columbia pink salmon (*Oncorhychus gorbuscha*). Journal of the Fisheries Research Board of Canada. 21: 1101-1128.

MacKinnon, B. M. 1997. Sea Lice: a review. World Aquaculture 28: 5-10.

Margolis, L., G. W. Esch, J. C. Holmes, A. M. Kuris, and **G. A. Schad.** 1982. The use of ecological terms in parasitology (report of an *ad hoc* committee of the American Society of parasitologists). Journal of Parasitology 68: 131-133.

McLean, P. H., G. W. Smith, and **M. J. Wilson**. 1990. Residence time of the sea louse, *Lepeophtheirus salmonis* K., on Atlantic salmon, *Salmo salar* L., after immersion in fresh water. Journal of Fish Biology 37: 311-314.

Nagasawa, K. 1987. Prevalence and abundance of *Lepeophtheirus salmonis* (Copepod: Caligidae) on high-sea salmon and trout in the North Pacific Ocean. Bulletin of the Japanese Society of Science and Fisheries 53: 2151-2156.

Nagasawa, K. 2001. Annual changes in the population size of the salmon louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) on high-seas Pacific Salmon (*Oncorhynchus* spp.), and relationship to host abundance. Hydrobiologia 453/454: 411-416.

Naylor, R. L., J. Eagle, and **W. L. Smith**. 2003. A global industry with local impacts. Environment 45: 18-39.

Parker, R. R. 1965. Estimation of sea mortality rates for the 1961 brood-year Pink Salmon of the Bella Coola area, British Columbia. Journal of the Fisheries Research Board of Canada 22: 1523-1554.

Parker, R. R., and **L. Margolis**. 1964. A new species of parasitic copepod, *Caligus clemensi* sp. nov. (Caligoida: Caligidae), from pelagic fishes in the coastal waters of British Columbia. Journal of the Fisheries Research Board of Canada 21: 873-889.

Parker, R. R., and **W. E. Vanstone**. 1966. Changes in chemical composition of central British Columbia Pink Salmon during early sea life. Journal of the Fisheries Research Board of Canada 23: 1353-1384.

Parker, R. R., and **R. J. LeBrasseur**. 1974. Ecology of early sea life, pink and chum juveniles. Pages 161-171 *in* Proceedings of the 1974 Northeast Pacific Pink and Chum Salmon Workshop. *Edited by* D. R. Harding. Department of the Environment, Fisheries, Vancouver, British Columbia.

Pearcy, W. G. 1992. Ocean Ecology of North Pacific Salmonids. University of Washington Press, Seattle. 179 pages.

Pike, A. W., and **S. L. Wadsworth.** 1999. Sealice on salmonids: their biology and control. Advanced Parasitology 44: 234-337.

Poole, W. R., D. T. Nolan, T. Wevers, M. Dillane, D. Cotter, and **O. Tully**. 2003. An ecophysiological comparison of wild and hatchery-raised Atlantic salmon (*Salmo salar* L.) smolts from the Burrishoole stsyem, western Ireland. Aquaculture 222: 301- 314.

Scott, W. B., and **E. J. Crossman**. 1973. Freshwater fishes of Canada (reprinted 1990). Bulletin of the Fisheries Research Board of Canada 184. 966 pages.

Schram, T. A., J. A. Knutsen, P. A. Heuch, and **T. A. Mo**. 1998. Seasonal occurrence of *Lepeophtheirus salmonis* and *Caligus elongatus (*Copepoda: Caligidae) on Sea Trout (*Salmon trutta*), off southern Norway. ICES Journal of Marine Science 55: 163-175.

Tully, O., W. R. Poole, and **K. F. Whelan**. 1993. Infestation parameters of *Lepeophtheirus salmonis* (Kroyer) (Copepod: Caligidae) parasitic on Sea Trout, *Salmo trutta* L., off the west coast of Ireland during 1990 and 1991. Aquatic Fisheries Management 24: 545-555.

White, H. C. 1940. "Sea Lice" *(Lepeophtheirus salmonis)* and death of salmon. Journal of the Fisheries Research Board of Canada 5: 172-175.

Wootten, R., J. W. Smith, and **E. A. Needham**. 1982. Aspects of the biology of the parasite copepods *Lepeophtheirus salmonis* and *Caligus elongatus* on farmed salmonids, and their treatment. Proceedings of the Royal Society of Edinburgh 81B: 185-197.

Zar, J. 1996. Biostatistical analysis. Prentice-Hall, New Jersey. 620 pages

Received 30 June 2003
Accepted 8 January 2004

Notes

First Record of the Deepwater Sculpin, *Myoxocephalus thompsonii,* from George Lake in Whiteshell Provincial Park, Manitoba

L. Murray[1], M. H. Papst[2], and J. D. Reist[2]

[1]Department of Zoology, University of Manitoba, Winnipeg, Manitoba R3T 2N2 Canada
[2]Freshwater Institute, Department of Fisheries and Oceans, 501 University Crescent, Winnipeg, Manitoba R3T 2N6 Canada

Murray, L., M. H. Papst, and J. D. Reist. 2003. First record of the Deepwater Sculpin, *Myoxocephalus thompsonii,* from George Lake in Whiteshell Provincial Park, Manitoba. Canadian Field-Naturalist 117(4): 642-644.

Two adult female specimens of Deepwater Sculpin, *Myoxocephalus thompsonii,* were collected by gillnet from George Lake near Point Du Bois, Manitoba, 36.8 km east of Lac Du Bonnet on 21 September 2000. This constitutes the first confirmed occurrence of the species in George Lake. The only other Manitoba lakes with known populations of Deepwater Sculpin are Lake Athapapuskow and West Hawk Lake. Deepwater Sculpins have also been collected from Reindeer Lake; however, these individuals were collected from the deeper Saskatchewan side of the lake.

Key Words: Deepwater Sculpin, *Myoxocephalus thompsonii,* George Lake, Manitoba.

Two adult Deepwater Sculpins *(Myoxocephalus thompsonii)* were collected by gillnet in the deepest region of George Lake, Manitoba (50°15.855'N, 95°28.521'W) on 21 September 2000. One Lake Whitefish *(Coregonus clupeaformis),* seven Lake Trout *(Salvelinus namaycush)* and 74 Shortjaw Cisco *(Coregonus zenithicus)* were captured in the same net as the two sculpins.

The collection site consisted of the deep basin at the north end of the lake (Figure 1). The net was set at

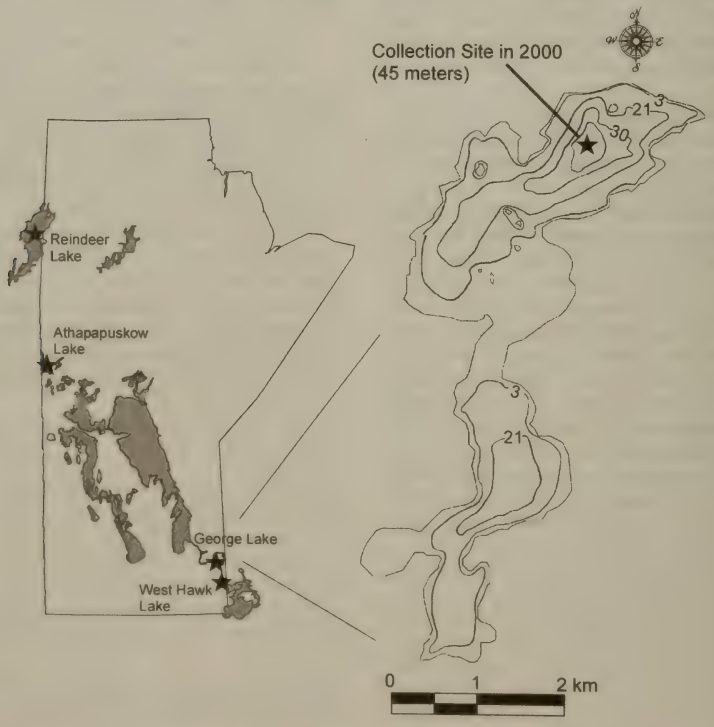


Figure 1. Deepwater Sculpin *(Myoxocephalus thompsonii)* distribution in Manitoba and adjacent Saskatchewan including the George Lake collection site (depth in meters).

TABLE 1. Characteristics of four species of freshwater sculpin found in Manitoba and two specimens of Deepwater Sculpin collected from George Lake, Manitoba.

	Average Total Length (mm)	Number of Preopercular Spines	First Dorsal Fin Rays (Range)	Second Dorsal Fin Rays (Range)	Anal Fin Rays (Range)	Pectoral Fin Rays (Range)	Pelvic Fin Rays (Range)	Gap Between Dorsal Fins	Head Length (% of Total Length)	Dorsal Colour Pattern
Mottled Sculpin, *Cottus bairdi*[1]	76	3	7 to 9	16 to 19	10 to 14	13 to 17	4 rarely 3	small	22.2 - 28.9	2-3 saddle marks
Spoonhead Sculpin, *Cottus ricei*[1]	51-64	2,3 or 4	7 to 10	15 to 18	12 to 16	14 to 16	1 spine, 4 rays	small	23.4-30	4 saddle marks
Slimy Sculpin, *Cottus cognatus*[1]	76	3	7 to 9	14 to 19	10 to 14	12 to 16	1 spine, 3 rays	small	22.0-27.9	2 saddle marks
Deepwater Sculpin[1]	50-100	4	7 to 10	11 to 16	11 to 16	15 to 18	1 spine, 3 rays	large	25.9-30.2	4-7 saddle marks
George Lake specimen Number 47255[2]	83.2	4	8	13	13	16	1 spine, 3 rays	large	28.4	5 faint saddle marks
George Lake specimen Number 47256[2]	78.5	4	8	14	14	17	1 spine, 3 rays	large	29.7	5 faint saddle marks

[1] Range of counts and common characteristics provided by Scott and Crossman (1973).
[2] *Myoxocephalus thompsonii*, ID 47255 and 47256 deposited in Fish Museum Collection, Department of Zoology, University of Manitoba, Winnipeg.

approximately 45 m in depth over a mud bottom. The net was 120 m in length and 1.83 m deep with 20 m panels ranging in mesh size from 10 to 25 mm. The two Deepwater Sculpins were caught in the 10 mm mesh panel after a 14.75-hour overnight set. The previous maximum recorded depth for the lake was 38.7 m and the mean depth was 11.9 m (Gibson and Johnson 1969*). The deep north basin is approximately 0.125 km^2 in area with gradually sloping north and south sides and steep sloping east and west sides. Deepwater Sculpins are commonly found at a depth of 73 m or greater in the Great Lakes; however, there are reports of their collection at 44 m from Lake Michigan (Scott and Crossman 1973).

The two sculpins were tentatively identified in the field as Deepwater Sculpins based on having four preopercular spines. The specimens were placed on ice for travel and frozen once in Winnipeg. A key and descriptions of the sculpins of North America from Scott and Crossman (1973) were used to confirm the identifications of the thawed specimens. The two specimens had the margin of their gill membranes free of the isthmus, four preopercular spines of which the upper two were directed backwards and the lower two downwards, and two dorsal fins separated by a distinct gap; all characters diagnostic of Deepwater Sculpins but absent in other sculpins found in Manitoba (Scott and Crossman 1973). All characteristics of the two George Lake specimens were in the limits of variation for Deepwater Sculpins (Table 1). Two characteristics, number of preopercular spines and the gap between dorsal fins, differentiated these fish from all other possible sculpin species known from Manitoba.

The Deepwater Sculpin and the marine Fourhorn Sculpin *(Myoxocephalus quadricornis)* have been the focus of several taxonomic studies. McAllister (1961) considered the two taxa to be distinct species. Hubbs and Lagler (1964) proposed a subspecific designation for the North American freshwater form of Deepwater Sculpin, referring to it as *Myoxocephalus quadricornis thompsonii*. The subspecific designation was accepted by Bailey et al. (1970) and McPhail and Lindsey (1970). The issue was revisited by McAllister and Aniskowicz in 1976 and McAllister et al. in 1978 and based on differences between morphological characters the two forms were again considered to be distinct species. The common name (Deepwater Sculpin) and the scientific name *(Myoxocephalus thompsonii)* were accepted by the American Fisheries Society in 1991 (Robins et al. 1991).

Deepwater Sculpins are distributed in lakes from southwestern Quebec, through the Great Lakes region to Manitoba, northern Saskatchewan, and north to Great Slave and Great Bear lakes in the Northwest Territories (Parker 1988). An isolated population was also reported from southern Alberta (McAllister and Wells 1980). Deepwater Sculpins have previously been identified from West Hawk Lake, and Lake Athapapuskow in Manitoba and from the Saskatchewan side of Reindeer

Lake, commonly being found in the stomachs of Lake Trout and Burbot *(Lota lota)* [K. W. Stewart, University of Manitoba, Department of Zoology, personal communication]. In 1969 a single sculpin was found in the stomach of a Lake Trout caught from George Lake, Manitoba. However, the specimen was not identified to species and was not kept for future examination (Gibson and Johnson 1969*). Our report confirms the presence of the Deepwater Sculpin in George Lake, Manitoba. Furthermore, this species may be found in other small lakes throughout its range provided they are of suitable depth (e.g., > 45 m) for this species to inhabit. The specimens were deposited in the University of Manitoba, Zoology Department, fish museum collection.

A new record of Deepwater Sculpin is important because it adds to our limited knowledge about the distribution of this species. This lack of information is partly due to the difficulty associated with collecting this species because of the specialized gear that is required and their preference towards deepwater habitat. Because of this and their disjunct distribution, the greater number of recorded occurrences we have will help us to better understand the reasons for their current distribution. This information may also be useful to glaciologists studying the previous locations of glacial lakes by examining the current distributions of glacial relict species such as sculpins.

Acknowledgments

We thank K. W. Stewart for confirmation of our identification and further information on the distribution of Deepwater Sculpins in Manitoba. Nathan Lovejoy provided space for these specimens in the University of Manitoba, Zoology Department fish museum collection. We also thank the two anonymous reviewers of this paper for their suggestions.

Documents Cited

Gibson, R. J., and **L. J. Johnson.** 1969. A limnological investigation of George Lake (Whiteshell Provincial Park) in 1967. Manitoba Department of Mines and Natural Resources, Fisheries Branch, Manuscript Report 69-3. 48 pages.

Literature Cited

Bailey, Reeve M., J. E. Fitch, E. S. Herald, E. A. Lachner, C. C. Lindsey, C. R. Robins, and **W. B. Scott.** 1970. A list of common and scientific names of fishes from the United States and Canada. American Fisheries Society Special Publication. 1970: 6.

Hubbs, C. L., and **K. F. Lagler.** 1964. Fishes of the Great Lakes region. University of Michigan Press, Ann Arbor, Michigan. 213 pages.

McAllister, D. E. 1961. The origin and status of the deepwater sculpin, *Myoxocephalus thompsonii,* a Nearctic glacial relict. Bulletin of the National Museum of Canada (Contributions to Zoology 1959) 172: 44-65.

McAllister, D. E., and **J. Aniskowicz.** 1976. Vertebral number in North American Sculpins of the *Myoxocpehalus quadricornis*-Complex. Journal of the Fisheries Research Board of Canada 33: 2792-2799.

McAllister, D. E., and **L. Wells.** 1980. *Myoxocephalus thompsoni* (Girard). Page 827 *in* Atlas of North American freshwater fishes. *Edited by* D. S. Lee, C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer Jr. North Carolina State Museum of Natural History, Biological Survey Publication. 1980-12. 854 pages.

McAllister, D. E., R. Murphy, and **J. Morrison.** 1978. The complete minicomputer cataloguing and research system for a museum. Curator 21: 63-92.

McPhail, J. D., and **C. C. Lindsey.** 1970. Freshwater fishes of northwestern Canada and Alaska. Fisheries Research Board of Canada Bulletin 173. 381 pages.

Parker, B. J. 1988. Status of the Deepwater Sculpin, *Myoxocephalus thompsoni,* in Canada. Canadian Field-Naturalist 102: 126-131.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and **B. Scott.** 1991. Common and scientific names of fishes from the United States and Canada. American Fisheries Society Special Publication 20: 1-183.

Scott, W. B., and **E. J. Crossman.** 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184. 966 pages.

Received 2 May 2001
Accepted 26 April 2004

Coyote, *Canis latrans* – Rio Grande Turkey, *Meleagris gallopavo intermedia,* Interactions

BRIAN L. SPEARS[1], WARREN B. BALLARD[1], MARK C. WALLACE[1], ROGER D. APPLEGATE[2] and PHILLIP S. GIPSON [3]

[1]Department of Range, Wildlife, and Fisheries Management, Texas Tech University, Box 42125, Lubbock, Texas 79409 USA
[2]Kansas Department of Wildlife and Parks, 1830 Merchant, Box 1525, Emporia, Kansas 66801 USA
[3]Kansas Cooperative Fish and Wildlife Research Unit, 205 Leasure Hall, Kansas State University, Manhattan, Kansas 66506 USA

Spears, Brian L., Warren B. Ballard, Mark C. Wallace, Roger D. Applegate, and Phillip S. Gipson. 2003. Coyote, *Canis latrans* – Rio Grande Turkey, *Meleagris gallopavo intermedia* interactions. Canadian Field-Naturalist 117(4): 645-647.

Coyotes (*Canis latrans*) are widely known to be predators of Wild Turkeys (*Meleagris gallopauo* sspp.). We describe two observations of single Coyotes coming within 10 m of feeding Wild Turkey flocks without attempting to predate them in Stevens County, Kansas. We relate these observations to Coyote predation on turkeys and mobbing behavior.

Key Words: Coyotes, *Canis latrans*, Kansas, Rio Grande Turkeys, *Meleagris gallopavo intermedia,* mobbing behavior.

Coyotes (*Canis latrans*) are widely known to be predators of Wild Turkeys (*Meleagris gallopauo* sspp.) (Ransom et al. 1987; Miller et al. 1992; Chamberlain et al. 1996; Hubbard et al. 1998; Miller et al. 1998). Coyotes also appear to be significant predators of Wild Turkeys in the rolling plains of Texas and Kansas (Figure 1). However, conditions under which Coyotes prey upon turkeys are poorly understood. We describe two observations of single Coyotes coming within 10 m of feeding Wild Turkey flocks without attempting to attack, in Stevens County, Kansas, and discuss the relevance of these observations in relation to avian mobbing behavior. We also describe a direct observation of Wild Turkey mobbing behavior, and present data demonstrating increased Coyote predation on Wild Turkeys as the latter become independent from intraspecific flocks during the breeding season.

Methods and Study Area

In January to early February 2000 and 2001 Wild Turkeys were baited with whole-kernel corn in an area in western Stevens County, Kansas, to facilitate drop-net trapping (Baldwin 1947). The area was contained by and within 50 m of the west (north) bank of the Cimarron River. Immediate habitat consisted of understory vegetation including Sand Bluestem (*Andropogon hallii*), Blue Grama (*Bouteloua gracilis*), Dropseed (*Sporobolus cryptandrus*), Sand Lovegrass (*Eragrostis trichodes*), Prairie Sandreed (*Calamovilfa longifolia*), Western Ragweed (*Ambrosia psilostachya*) and Buffalo Grass (*Buchloe dactyloides*). Eastern Cottonwood (*Populus deltoides*) and Tamarisk (*Tamarix chinensis*) groves were found in the river basin. Most of the aforementioned grasses, as well as Sagebrush (*Artemisia filifolia*), rabbitbrush (*Chrysothamnus* sp.), Snakeweed (*Gutierrezia sarothrae*) and Plains Yucca (*Yucca glauca*) covered the fields and hills surrounding the Cimarron River corridor. Precipitation averaged approximately 42.16 cm/year and was concentrated from April to September (Cable et al. 1996). Crop fields occurred within 100 m west of the riverbank, and are rotationally planted with corn and winter wheat. A major part of the Cimarron River in this area was dry at the surface, except for occasional flooding.

Both observations took place from a blind at the same bait site. The site was within the daily home range of a wintering turkey flock (B. Spears, unpublished data). Lone Coyotes were observed and Coyote groups were heard on a regular basis in and around the area.

Results

On 4 February 2000 at 07:33 a flock of >40 turkeys arrived at bait underneath a drop net. At 07:37 a lone Coyote arrived, seemingly headed to another area. Several of the turkeys were alerted and watched the Coyote as the others continued to investigate the bait. After a several-second pause, the Coyote made a short run (<5 m) at the flock. The closest turkeys moved not more than 10 m further into the flock, which alerted the rest of the individuals. After the short charge, the Coyote stopped, turned around, and continued on its previous heading. Within 1 min the turkey flock moved under the net and most began to feed heavily.

At 07:55 on 11 January 2001, a flock of 63 individuals arrived on bait, coming directly from roost. Fourteen of the birds had been transmitter-equipped at the same trap site on 10 February 2000. At 08:35 the last individual ceased feeding, and the majority of the birds loafed in a large group among cottonwoods adjacent to the bait. Several individuals began moving up the west bank, and were startled and ran a short distance back toward the others and stopped. A lone Coyote was then observed moving east toward the flock. The Coyote continued to move east down the bank along a game trail, in between several turkeys and past the bait. Alerted turkeys stood watching as the Coyote moved between them, at points within 5 m. At no time did any of the turkeys disperse nor did the Coyote

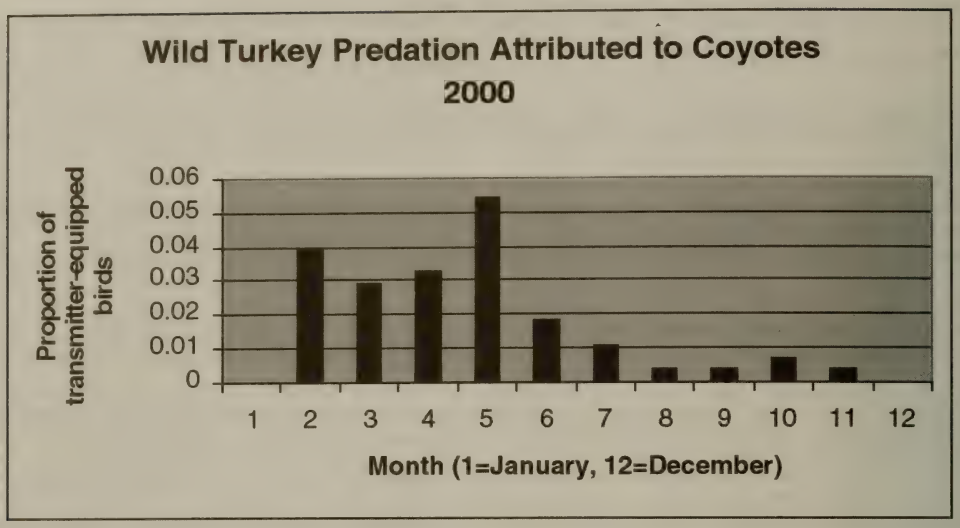


FIGURE 1. Proportions of transmitter-equipped Wild Turkey mortalities attributed to Coyotes in 2000 (n=56).

turn its head toward or make any sort of aggressive advance toward an alerted individual. The Coyote then continued at a walking pace into the river corridor. Many of the turkeys returned to feeding shortly thereafter, and then followed as the flock slowly wandered off the bait area into the river corridor. Lone Coyotes have subsequently been observed using the same or adjacent parallel game trails through the bait area.

Discussion

As evidenced by these observations, we hypothesize that Coyotes are deterred from attacking Wild Turkey flocks. A major deterrent presumably is the ability of a turkey flock to mob Coyotes. Wild Turkey mobbing behavior was witnessed by Roilond and Brent McDonald, two residents of Morton County, Kansas (personal communication). They witnessed a turkey flock mob a lone Coyote that attempted to attack an individual within the flock. The occurrence took place on the north edge of the riparian corridor of the Cimarron River, several years prior to, and approximately 10 km southwest of, the above observations. Several turkeys joined in the behavior, and they concluded that the Coyote had been physically injured in some manner before it retreated.

Our observations of Coyote behavior near flocks of turkeys differ markedly from an observation of a lone Coyote that approached a single turkey at Fort Riley Military Base, Kansas. On 9 May 1998, Irwin Hoogheem (personal communication) stopped his automobile at 11:00 to watch a lone Coyote crossing a soybean field along the eastern boundary of Fort Riley Military Base. The Coyote, wearing a radio-collar, was part of a family group that commonly hunted around the field; it was trotting toward a lone turkey feeding among young soybeans that were 10-12 cm high. The Coyote suddenly ran directly at the turkey when it was about 20 m away. The turkey fled and started to fly when the Coyote was within 5-10 m; it flew approximately 250 m across the field to a large Sycamore (*Platanus occidentalis*) tree and perched 25-30 m above the ground. The Coyote slowed to a trot and followed the flight path of the turkey to the tree. The Coyote lay down near the base of the tree and watched the turkey. Hoogheem observed the animals for 30 minutes; the turkey remained perched in the tree and the Coyote was vigilant on the ground.

Mobbing behavior has been widely observed throughout the avian class, as well as in mammals and fish (Shed 1978; Earnhardt 1989; Ridall 1998), with larger groups of individuals appearing to produce more successful mobbings (Earnhardt 1989). Several reasons for mobbing have been proposed. First, mobbing may be a direct attempt to reduce individual risk of predation by causing a predator to move out of the area through intimidation and harassment (Shed 1978; Wahl 1979; Earnhardt 1989; Ridall 1998). Second, mobbing may be a form of "perception advertisement", that is, the predator is deterred from predation attempts where its prey has discovered its presence (Earnhardt 1989; Ridall 1998). Third, passive mobbing, or indirect mobbing, may be an evolutionary technique to locate and track a predator. Birds apparently remember previous locations of a predator, and even continue to mob the location in the absence of the predator (Altmann 1954; Ridall 1998). Individuals also may use mobbing to alert and recruit other mobbers, or to aid distressed victims (Earnhardt 1989; Ridall 1998) or protect young through predator distraction (Wahl 1979). Finally, mobbing may be a cultural transmission device in which

parents teach their young about a specific predator (Earnhardt 1989; Ridall 1998). Birds appear to have the ability to differentiate among predators (Altmann 1954; Shed 1978; Wahl 1979; Ridall 1998), and may communicate the type of predator vocally. They also may have the ability to differentiate between predator behaviors (i.e., hunting vs. loafing) and mob accordingly (Ridall 1998). It has also been proposed that avian mobbing behavior evolved through a combination of several separate behaviors including attack, investigation, and flight behaviors (Shed 1978).

Although many avian species have been classified as "winter mobbers", "summer mobbers", or "year-round mobbers" (see Shed 1978 and Earnhardt 1989 for extensive reviews), avian mobbing seems to increase as breeding seasons progress, and to peak at peak breeding times (Shed 1978; Wahl 1979; Earnhardt 1989; but see Ridall 1998). However, Shed (1978) also found a high incidence of mobbing during winter in resident flocking species that maintained winter territories. Wild Turkey mobbing would appear to increase and be more efficient during winter months when turkeys are in larger flocks and maintain a mutual home range.

Wild Turkeys may become more vulnerable to predation during spring and summer months. Individuals break from their flocks in late winter and early spring and develop separate or small-group summer home ranges. Nesting hens actively avoid other individuals while searching for nest sites and during egg laying (Healy 1992). Factors increasing mortalities due to predation may include dispersal and migration movement through unfamiliar habitats and increased visibility due to displaying and breeding behaviors. However, we hypothesize that a major factor is the decreased protection occasioned by reduced vigilance without a surrounding flock.

Wild Turkey predation attributed to Coyotes in the high/rolling plains of Kansas and Texas in 2000 increased during the breeding season, with a peak during peak breeding and nesting months (Figure 1). In other areas proportions of kills attributed to Coyotes subsequently decrease as brooding hens began to reflock with other hens and males (Moody and Woodcock 1995).

Trends in turkey mortalities attributed to Coyote predation seem to follow those of a decrease and subsequent increase in flock numbers. Therefore, we speculate that flocking behavior provides turkeys with a detection and deterrent system to facilitate escape from predation when confronted by Coyotes.

Acknowledgments

The study was funded by Kansas Department of Wildlife and Parks, Federal Aid in Wildlife Restoration Project W-54-R, Texas Parks and Wildlife Department, the National Wild Turkey Federation, and the State Superfund of the Texas Chapter of the National Wild Turkey Federation. This is Texas Tech University College of Agricultural Sciences and Natural Resources Technical Publication T-9-894.

Literature Cited

Altmann, S. 1954. Avian mobbing behavior and predator recognition. M.A. thesis, University of California, Berkeley, California, USA.

Baldwin, W. P. 1947. Trapping turkeys in South Carolina. Journal of Wildlife Management 11: 24-36.

Cable, T. T., S. Seltman, and **K. J. Cook.** 1996. Birds of Cimarron National Grassland. USDA Forest Service General Technical Report RM-GTR-281.

Chamberlain, M. J., D. A. Miller, B. D. Leopold, and **G. A. Hurst**. 1996. Predation rates on wild turkey hens in a hardwood bottomland forest and a mixed forest in Mississippi. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 50: 428-435.

Earnhardt, R. 1989. Avian mobbing behavior: influencing factors, taxonomic distribution, and function. M.Sc. thesis, University of North Carolina, Charlotte, North Carolina, USA.

Healy, W. M. 1992. Behavior. Pages 46-65 *in* Wild turkey: biology and management. *Edited by* J. G. Dickson. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Hubbard, M. W., D. L. Garner, and **E. E. Klaas**. 1998. Factors influencing wild turkey hen survival in southcentral Iowa. Journal of Wildlife Management 63: 731-738.

Miller, D. A., L. W. Burger, B. D. Leopold, and **G. A. Hurst**. 1998. Survival and cause specific mortality of wild turkey hens in central Mississippi. Journal of Wildlife Management 62: 306-313.

Miller, J. E., and **B. D. Leopold**. 1992. Population influences: predators. Pages 119-128 *in* Wild turkey: biology and management. *Edited by* J. G. Dickson. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Moody, A., and **C. E. Woodcock**. 1995. The influence of scale and the spatial characteristics of landscapes on landcover mapping using remote sensing. Landscape Ecology 10: 363-379.

Ransom, D., Jr., O. J. Rongstad, and **D. H. Rusch**. 1987. Nesting ecology of Rio Grande turkeys. Journal of Wildlife Management 51: 435-439.

Ridall, R. 1998. The effect of sympatry on avian mobbing behavior. M.Sc. thesis East Tennessee State University, Johnson City, Tennessee, USA.

Shed, D. H. 1978. The adaptive significance of avian mobbing. Ph.D. dissertation Cornell University, New York, New York, USA.

Wahl, C. R. 1979. Seasonal, interspecific, and intraspecific variation in the mobbing response of desert birds to different predator types. M.Sc. thesis New Mexico State University, Las Cruces, New Mexico, USA.

Received 27 April 2001
Accepted 6 April 2004

Extralimital Sighting of a Polar Bear, *Ursus maritimus*, in Northeast Saskatchewan

MICHAEL A. GOODYEAR

Churchill Northern Studies Centre, Box 610, Churchill, Manitoba R0B 0E0 Canada; e-mail: goodyear@churchillmb.net

Goodyear, Michael A. 2003. Extralimital sighting of a Polar Bear, *Ursus maritimus*, in northeastern Saskatchewan. Canadian Field-Naturalist 117(4): 648-649.

The first documented occurrence of a Polar Bear (*Ursus maritimus*) in northeastern Saskatchewan, 420 km from the western coast of Hudson Bay, is described. The bear was most likely a sub-adult male in fair condition, with respect to body fat. Early break-up of ice on Hudson Bay in the spring of 1999 may have contributed to this significant extralimital sighting.

Key Words: Polar Bear, *Ursus maritimus*, distribution, behaviour, Saskatchewan.

On 12 September 1999, Tom Estes and Ray Woolrich of Bartlesville, Oklahoma, video-documented the occurrence of a Polar Bear, *Ursus maritimus*, while fishing on Burnett Lake (59° 02' N, 102° 18' W), a small, remote lake near the Saskatchewan-Manitoba border. At 14:00, approximately 1.2 km from shore, a Polar Bear swam to within 18-27 m of their boat while Estes videotaped the encounter. The bear was seen earlier at some distance, but was initially mistaken for a gull. The bear was undeterred by noise from the outboard motor and, despite the observers relocating another 1 km down the lake, continued to follow the boat. The pair retreated once again but, before returning to camp, they attempted to lure the bear away from the area by meandering around some nearby bays and islands. The bear was not seen for the remainder of their trip or by subsequent fishing parties. A copy of the videocassette was forwarded to the Canadian Wildlife Service in Edmonton, Alberta, where it was confirmed that the bear was most likely a sub-adult male in fair condition, with respect to body fat (D. Andriashek and N. Lunn, Canadian Wildlife Service, 5320-122 St., Edmonton, Alberta T6H 3S5, personal communication).

To the author's knowledge, this encounter represents the first confirmed sighting of a Polar Bear in Saskatchewan. The straight-line distance from the nearest point on the Hudson Bay coast to Burnett Lake is approximately 420 km through sparse to dense boreal forest and lakes. While inland sightings of Polar Bears 100-150 km from coast, especially within the Hudson Bay Lowland denning area, are common (Derocher and Stirling 1990), similar reports of extralimital sightings in the literature are rare. In 1938, a sub-adult male was shot at the mouth of the Peribonka River, Lac St. Jean, Quebec, 640 km inland from James Bay (Jackson 1939). In the mid-1990s a Polar Bear was reported destroyed at the Tsiigehtchic, North West Territories (Arctic Red River) landfill, 190 km from the mouth of the Mackenzie River, but this could not be independently verified. Packard (1886) speculated that Polar Bears may have historically ranged as far down the eastern coast as Maine.

Sightings such as these are extremely rare, and serious attempts to monitor the movement of Polar Bears have been limited to the past three decades. Traditional knowledge may prove valuable in providing a historical context of the frequency of inland movement, but such information is rarely documented in the scientific literature. It is important, therefore, to record extralimital sightings in order to better understand Polar Bear movements during the ice-free season, especially with reference to the potential effects of longer ice-free periods on Hudson Bay associated with climate change (Stirling et al. 1999). The break-up of ice on Hudson Bay during the spring of 1999 was earlier than normal and this may have influenced the bear's movements. Many bears were forced ashore farther north than normal, resulting in sightings in areas not usually frequented by bears at that time of the year (Cam Elliott, Parks Canada, Box 668, Churchill, Manitoba R0B 0E0). It is possible that this bear may have travelled up one of several river systems (e. g., the Seal or Thlewiaza) before continuing overland by some unknown route to Saskatchewan, but this is not known.

Acknowledgments

The assistance of Tom Estes and Ray Woolrich in the description of this occurrence was greatly appreciated. The author also wishes to thank Dennis Andriashek and Nick Lunn for providing comments on the video footage. Peter Scott and Jack Dubois provided comments on early drafts. Investigations of this sighting were made by the author while in the employ of Saskatchewan Environment and Resource Management, La Ronge, Saskatchewan.

Literature Cited

Derocher, A. E., and **I. Stirling**. 1990. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. Canadian Journal of Zoology 68: 1395-1403.

Jackson, H. H. T. 1939. Polar bear in the Lake St. John District, Quebec. Journal of Mammalogy 20: 253.

Packard, A. S. 1886. The former southern limits of the white or polar bear. American Naturalist 20: 655-659.

Stirling, I., Lunn, N., and **J. Iacozza**. 1999. Long-term trends in the population of polar bears in western Hudson Bay in relation to climatic change. Arctic 52: 294-306.

Received 1 November 2001
Accepted 16 April 2004

Dryopteris goldiana × *D. intermedia*, a Natural Fern Hybrid New to Canada

PAUL M. CATLING

Agriculture and Agri-Food Canada, Central Experimental Farm, Ottawa, Ontario K1A 0C6 Canada

Catling, Paul M. 2003. *Dryopteris goldiana* × *D. intermedia*, a natural fern hybrid new to Canada. Canadian Field-Naturalist 117(4): 649-651.

The rare fern hybrid *Dryopteris goldiana* × *D. intermedia* is reported for the first time from Canada on the basis of a collection from eastern Ontario. The plant occurred in rich deciduous woods in an extensive seepage area at the base of a slope. The immediate vicinity had an unusually high floristic diversity and 25 associated vascular plants are listed. Distinguishing characteristics of the hybrid are outlined.

Key Words: *Dryopteris goldiana* × *D. intermedia*, Goldie's Fern, Evergreen Wood Fern, hybrid, conservation, biodiversity, bioindicator, Canada.

Areas of occurrence of natural hybridization of native species should be preserved as part of a dynamic ecosystem (Whitham and Maschinski 1996). Such areas containing plant hybrids are often "hot spots of ecological and evolutionary activity" (Whitham 1991). Hybrids are important with regard to genetic diversity and the conservation of evolutionary potential, and in some cases they serve as important indicators of areas of high biodiversity (Whitham 1991). They also provide opportunities for research aimed at testing evolutionary and ecological hypotheses. Natural hybridization has played a significant role in the evolution of the fern genus *Dryopteris* (Evans and Wagner 1964). The distribution and frequency of *Dryopteris* hybrids are important in determining relationships between the taxa for classification purposes, and an understanding of hybrids and their characteristics is essential for identification.

During a study of the floristic composition of the Rigaud Headwaters ANSI (Area of Natural and Scientific Interest) in eastern Ontario, a plant was found that had characteristics of both Goldie's Fern, *Dryopteris goldiana* (Hook. ex Goldie) A. Gray, and Evergreen Wood Fern, *Dryopteris intermedia* (Muhlenb. ex Willd.) A. Gray. Because such a hybrid had not previously been found in Canada (Cody and Britton 1989), the Canadian floristic literature provided no means of identification of the plant. Its identity as a hybrid of the two species it resembled was later determined with publications covering areas in the United States and specialized literature on fern hybrids. The identification was confirmed by J. D. Montgomery, a specialist in classification and identification of *Dryopteris* taxa.

Voucher:

Ontario: Glengarry Co.: Kenyon twp.: 10 km NE of Maxville, approx. 31 G/7 18T 519450 5021750, 2 Oct. 2001, P.M. Catling (DAO).

Distribution and ecology

Dryopteris goldiana occurs throughout a large portion of eastern North America, reaching its northern limit in southeastern Canada where it occurs from New Brunswick west to southern Quebec and southern Ontario (Cody and Britton 1989; Carlson and Wagner 1982). *Dryopteris intermedia* is more widespread in eastern North America and in Canada where it occurs from Newfoundland west to northwestern Ontario (Cody and Britton 1989; Carlson and Wagner 1982). Although a number of hybrids involving each of these two species have been reported from Canada (Cody and Britton 1989), a cross between *D. goldiana* and *D. intermedia* is known only from the United States where there are reports from Michigan, New Jersey, New York, North Carolina, Ohio and Vermont. It is generally considered to be rare (Wherry 1961; Montgomery 1982; Thorne and Thorne 1989). After 10 years of studying *Dryopteris*, Evans and Wagner (1964) noted that they had examined thousands of plants in dozens of localities without finding this cross, which they regarded as "one of the most unusual of the rare hybrid woodferns".

Habitat

Dryopteris goldiana × *D. intermedia* is reported to occur near the bottom of moist limy talus (Thorne and Thorne 1989). At the eastern Ontario location the plant occurred in rich deciduous woods in an extensive seepage area at the base of a slope. The area is within the hilly Glengarry Till Plain and the vegetation in this region has developed over a substrate of sand and gravel. The forest was dominated by Black Maple (*Acer saccharum* Marshall ssp. *nigrum* (Michx. f.) Desmarais – 30%), Sugar Maple (*Acer saccharum* Marshall ssp. *saccharum* – 40%), Bitternut Hickory (*Carya cordiformis* (Wandenh.) K. Koch – 10%), White Ash (*Frax-*

inus americana L. – 10%), and American Basswood (*Tilia americana* L. – 10%). The trees were mostly about 75 years old, and light selective cutting probably occurred 40 years ago. Average Sugar Maple tree diameter at breast height (dbh) was about 33 cm and the maximum was 45 cm for White Ash and Basswood. The general area (approximately 30 × 100 m) at the base of the slope had an unusually high diversity of herbaceous species along with woody saplings of Ironwood (*Ostrya virginiana* (Miller) K. Koch) and maples. Dominant herbs included *Mitella diphylla* (Two-leaved Bishop's Cap), and the sedges *Carex platyphylla* J. Carey (Broad-leaved Sedge) and *Carex pedunculata* Muhlenb. ex Willd. (Long-stalked Sedge). Other frequent species observed during the autumn visit to the site included *Actaea pachypoda* Elliot (White Baneberry), *A. rubra* (Aiton) Willd. (Red Baneberry), *Adiantum pedatum* L. (Northern Maidenhair Fern), *Allium tricoccum* Aiton (Wild Leek), *Amphicarpa bracteata* (L.) Fern. (Hog Peanut), *Anemone acutiloba* (DC.) G. Lawson (Sharp-lobed Hepatica), *Athyrium filix-femina* (L.) Roth ex Mert. var. *angustum* (Willd.) G. Lawson (Northern Lady Fern), *Carex plantaginea* Lam. (Plantain-leaved Sedge), *Caulophyllum thalictroides* (L.) Michx. (Blue Cohosh), *Deparia acrostichoides* (Swartz) M. Kato (Silvery Glade Fern), *Diplazium pycnocarpon* (Spreng.) M. Brown (Narrow-leaved Spleenwort), *Dryopteris goldiana* (Hook. ex Goldie) A. Gray (Goldie's Fern), *Dryopteris intermedia* (Muhlenb. ex Willd.) A. Gray (Evergreen Wood Fern), *Eupatorium rugosum* Houtt. (White Snakeroot), *Gymnocarpium dryopteris* (L.) Newman (Oak Fern), *Maianthemum racemosum* (L.) Link (False Solomon's Seal), *Phryma leptostachya* L. (Fogfruit), and *Uvularia grandiflora* Sm. (Large-flowered Bellwort).

Identification Characteristics

Although rare, the *D. goldiana* × *D. intermedia* hybrid is not difficult to identify because it combines unique characters of both parents: the glands of *D. intermedia,* especially on the indusium, and the dark petiole scales of *D. goldiana*. The hybrid plant collected in eastern Ontario possessed both of these features. The blade, abruptly tapered at the tip (Figure 1), is distinctly bipinnate-pinnatifid at the base and the basal pinnules are shorter than the adjacent pinnules (Figure 1) so that the specimen keys to *D. intermedia* in many texts (e.g., Montgomery and Wagner 1993). However, the sori are essentially on the midvein of the segments rather than between the midvein and the margin as is characteristic of *D. intermedia*. The basal pinnae are lanceolate or ovate rather than triangular or deltate, thus eliminating *D. clintoniana* (D. C. Eaton) Dowell and *D. cristata* (L.) A. Gray. The relatively abrupt tapering of the frond to the tip eliminates the *D. celsa* (Palmer) Knowlton, Palmer and Pollard × *intermedia* hybrid. Together the above characteristics

FIGURE 1. Silhouette of voucher specimen of *D. goldiana* × *D. intermedia* from eastern Ontario showing distinctive features including the abruptly tapered frond tip, bipinnate-pinnatifid frond base and basal pinnules shorter than the adjacent pinnules. The frond is 81 cm tall.

of the frond, glands, sori position, and scales distinguish the *D. goldiana* × *D. intermedia* hybrid from all other known *Dryopteris* hybrids. In a detailed study of *D. goldiana* × *D. intermedia*, Evans and Wagner (1964) emphasized that it looks like an unusually large individual of *D. intermedia* and often resembles *D. intermedia* more closely than *D. goldiana*.

Another hybrid woodfern involving *D. goldiana* was recently given a name, *Dryopteris* × *mickelii* Peck (*D. clintoniana* × *goldiana*), and was reported for the first time in the Ottawa district of eastern Ontario (Peck 2001; Cody 2002). This hybrid differs from the *D. goldiana* × *D. intermedia* hybrid in the fronds being pinnate-pinnatifid on the basal pinnae instead of bipinnate-pinnatifid. The recently described Correll's Woodfern, *Dryopteris correllii* Wagner (*D. carthusiana* (Villars) H. P. Fuchs × *D. goldiana*) is unlike *D. goldiana* × *D. intermedia* in being eglandular throughout (Evans and Wagner 1964; Wagner and Gilman 2001).

Additional information on the distinctive characteristics of *D. goldiana* × *D. intermedia* is available in Evans and Wagner (1964), Montgomery (1982), and Thorne and Thorne (1989).

Acknowledgments

The identification was confirmed by J. D. Montgomery. Useful comments were provided by W. J. Cody.

Literature Cited

Carlson, T. M., and **W. H. Wagner, Jr.** 1982. The North American distribution of the genus *Dryopteris*. Contributions of the University of Michigan Herbarium 15: 141-162.

Cody, W. J. 2002. *Dryopteris* × *mickelii* Peck, Simulated Log Fern, a newly named hybrid fern found in the Ottawa District. Trail & Landscape 36: 43-45.

Cody, W. J., and **D. M. Britton.** 1989. Ferns and fern allies of Canada. Agriculture Canada Research Branch Publication 1829/E. 430 pages.

Evans, A. M., and **W. H. Wagner, Jr.** 1964. *Dryopteris goldiana* × *intermedia*, a natural hybrid woodfern cross of noteworthy morphology. Rhodora 66: 255-266.

Montgomery, J. D. 1982. *Dryopteris* in North America – part II: the hybrids. Fiddlehead Forum (Bulletin of the American Fern Society) 9(4): 23-30.

Montgomery, J. D., and **W. H. Wagner Jr.** 1993. 9. *Dryopteris* Adanson. Pages 280-288 in Flora of North America Volume 2, Pteridophytes and Gymnosperms. Oxford University Press, New York.

Peck, J. H. 2001. Binomial for *Dryopteris clintoniana* × *goldiana*. American Fern Journal 91(1): 36-37.

Thorne, F., and **L. Thorne.** 1989. Henry Potter's field guide to the hybrid ferns of the northeast. Vermont Institute of Natural Science, Woodstock, Vermont.

Wagner, W. H., and **A. V. Gilman.** 2001. *Dryopteris correllii* hyb. nov. (*D. carthusiana* × *goldiana*), a rare woodfern hybrid from Vermont. American Fern Journal 91(1): 9-12.

Wherry, E. T. 1961. The fern guide – northeastern and midland United States and adjacent Canada. Doubleday and Co., New York. 318 pages.

Whitham, T. G. 1991. Conservation of hybrid plants. Science 254: 779-780.

Whitham, T. G., and **J. Maschinski.** 1996. Current hybrid policy and the importance of hybrid plants in conservation. Pages 103-112 *in* Southeastern rare and endangered plants, proceedings of the second conference, Flagstaff, Arizona, U.S.A. 11-14 Sept. 1995. *Edited by* J. Maschinski, H.D. Hammond and L. Holter. General technical Report. Rocky Mountain Forest and Range Experiment Station, U.S. Department of Agriculture.

Received 9 April 2002
Accepted 25 February 2004

New Records of the Eastern Red Bat, *Lasiurus borealis*, from Cypress Hills Provincial Park, Saskatchewan: A Response to Climate Change?

CRAIG K. R. WILLIS[1] and R. MARK BRIGHAM

Department of Biology, University of Regina, Regina Saskatchewan, S4S 0A2 Canada
[1]Current address: Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale, New South Wales, 2351, Australia; e-mail: cwillis2@pobox.une.edu.au (corresponding author).

Willis, Craig K. R., and R. Mark Brigham. 2003. New records of the Eastern Red Bat, *Lasiurus borealis*, from Cypress Hills Provincial Park, Saskatchewan: a response to climate change? Canadian Field-Naturalist 117(4): 651-654.

During the summer of 2001 we captured two Eastern Red Bats (*Lasiurus borealis*) in Cypress Hills Provincial Park, Saskatchewan. A possible explanation for this range extension is a warming trend since 1965 documented for the area.

Key Words: Eastern Red Bat, *Lasiurus borealis*, new records, global warming, Cypress Hills, Saskatchewan.

Eastern Red Bats (*Lasiurus borealis*) are a wide-ranging vespertilionid found throughout most of the United States, much of South America and in southern Canada from the east coast to approximately the mid-longitude of Saskatchewan in the west (Shump and Shump 1982; Saskatchewan Environment and Resource Management 2001; Figure 1). This species roosts almost exclusively in the open foliage of trees (Shump and Shump 1982; van Zyll de Jong 1985). It is usually found near forests, often roosting along for-

est edges, or in open areas where shade trees are present (Shump and Shump 1982). The Eastern Red Bat mates in the fall and gives birth to 1-5 pups (mean = 2.3) in the spring (Hamilton and Stalling 1972; Shump and Shump 1982). It is migratory and Canadian populations likely over-winter in the southern U.S., generally south of 40° N (Davis and Lidicker 1956), hibernating in the open foliage of trees or in tree cavities (Cowan and Guiget 1965). Of Canada's 19 species of bats, the red bat are the most easily identified because of their distinctive pelage. Dorsally, the Eastern Red Bat is rusty red in colour with whitish fur ventrally and a heavily furred interfemoral membrane. Indeed, the genus name *Lasiurus* literally means "hairy tail" (Shump and Shump 1982).

During the summer of 2001, while conducting research on bats in the West Block of Cypress Hills Provincial Park, Saskatchewan, we captured two Eastern Red Bats in mist nets. The first capture occurred at 23:30 on 24 July at a site 2.5 km east of the Saskatchewan-Alberta Border (49° 37.5'N, 110° 59'W) over the Battle Creek. The second capture occurred at 23:45 on 13 August, slightly further east, approximately 4.5 km from the Saskatchewan-Alberta border (49° 36'N, 110° 56'W), also over the Battle Creek.

For both bats we recorded sex, and age (adult or young of the year) was determined by examining the cartilaginous gap between the diaphysis of the metacarpal and proximal phalanx (Anthony 1988). Reproductive status was assessed by gentle palpation of the abdomen for pregnancy, expression of milk and bare patches around the nipples for lactation, and re-growth of fur around the nipples for post-lactation (Racey 1988). The individual captured in July was a non-reproductive adult female (mass = 14.5 g, forearm = 41.78 mm, tibia = 21.64 mm). The August individual was a reproductive female. She had bare nipples but milk could not be expressed so we cannot determine conclusively if she was in the late stages of lactation or early postlactation. Her body size was not measured.

The nearest record of *L. borealis* along the western fringe of its range is from Expanse, Saskatchewan, approximately 300 km to the east. This species has also been captured near Saskatoon, about 460 km northeast of the Cypress Hills, and one bat was captured in Calgary, Alberta. Van Zyll de Jong (1985) cites this occurrence of *L. borealis* west of Saskatchewan as accidental and suggests that this species' migratory wintering strategy may cause it to stray into territory outside its regular range. Our captures, however, suggest that this species is resident at least as far west as the Saskatchewan-Alberta border, for two reasons. First, one of the captures occurred in July, well outside the migration period. Barclay (1984) found that Red Bats moved through Delta Marsh, Manitoba, during spring and early fall but he never captured individuals during mid-summer. If the individual we captured was simply migrating through the Cypress Hills we would not expect to catch her in July. Second, the individual captured in August was likely lactating, and therefore still roosting with her pre- or newly volant pups nearby, which suggests that *L. borealis* reside and raise young in the Cypress Hills. More work is needed, however, to confirm the presence of a breeding population because the reproductive individual could have been an early migrant. The Hoary Bat (*Lasiurus cinereus*), a closely related species with a very similar life history (migratory, roosts in open foliage), is known to continue nursing pups quite late in the season. Separation occurs when pups are approximately seven weeks of age and migration begins (Koehler and Barclay 2000). Based on radio-telemetry data, some resident mother/adult Hoary Bat groups separate and leave the Cypress Hills by mid-August, but most remain in the area until later in the month. Some early migrants, which leave the area within a day or two of capture, pass through the Cypress Hills in mid-late August, as well (Willis, unpublished data). Red bats may follow a similar pattern of staggered migration, so we cannot conclude that the individual we captured was rearing pups in the Cypress Hills. Radio-telemetry studies will be important for determining the reproductive status and roosting requirements of this species if it is captured in the area again.

Bat diversity is affected by the availability of suitable roosting habitat (Humphrey 1975). In this sense, the Cypress Hills are one area where a relatively high diversity of bats, especially foliage roosting species like Eastern Red Bats, is expected. Compared with the open prairie, which surrounds the region for hundreds of kilometers, the Cypress Hills have abundant roosting opportunities. In addition, roosting in open foliage may allow red bats to be relatively flexible in their choice of roost trees. For example, in Kentucky, red bats roosted in 13 different hardwood species and, among these, showed no species-specific preference, although they avoided conifers (Hutchinson and Lacki 2000). Given this flexibility, and the fact that the red bat's known range is a relatively short distance (~ 300 km) to the east, one might expect to find this species in the Cypress Hills. However, in seven summers of sampling over the past decade (1991 – 1994 and 1999 – 2001) with roughly equal mist-netting effort, the records reported here are the first two for this species. By comparison, during the summers of 2000 and 2001 we captured over 25 Hoary Bats, over 30 Little Brown Bats (*Myotis lucifugus*), and over 30 Silver-haired Bats (*Lasionycteris noctivigans*) [Willis, unpublished data]. On the other hand, the relative abundance of some bat species may be underestimated based on mist-net captures alone. For example, in the Cypress Hills we know that Big Brown Bats (*Eptesicus fuscus*) are abundant because we capture 30-40 per year by trapping at Trembling Aspen (*Populus tremuloides*) cavity roosts, and observe hundreds more emerging from roosts, but we catch only 1-2 per year mist-netting over foraging areas along Battle Creek

FIGURE 1. The current Canadian range of the Red Bat, *Lasiurus borealis*. The black dot represents the Cypress Hills where two individuals were captured during summer 2001.

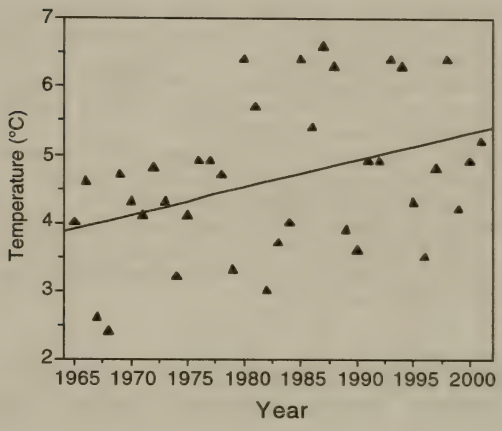


FIGURE 2. Mean minimum temperatures from 1965 to 2001 for May of each year, recorded from the Agriculture Canada Research Station at Onefour, Alberta, less than 50 km west of Cypress Hills, Saskatchewan. There is a significant warming trend (P=0.02, n=37, r^2=0.15), which could account for a range expansion of *Lasiurus borealis*.

[Willis, unpublished data]. Mist-net captures, then, may also underestimate Eastern Red Bats in the area.

One biologically relevant explanation for the rarity of red bats in the Cypress Hills could be this species' preference for deciduous trees over conifers (Hutchinson and Lacki 2000), which dominate much of the region's forest. This seems unlikely, however, given that Trembling Aspen are ubiquitous. Another explanation could be that the current presence of red bats is a response to climate change. The relatively high elevation of the Cypress Hills results in cold summer minimum temperatures compared to the surrounding prairie at similar latitudes, and nights with subfreezing temperatures are common especially in the spring. Red bats are known to occur in relatively cold areas in Canada, but do not range as far north as Hoary Bats (van Zyll de Jong 1985). Hoary Bats are common in the Cypress Hills, perhaps because of their larger body size and smaller body surface to volume ratio, which will result in lower rates of heat loss than red bats. Historically, red bats may have been prevented from exploiting the abundant roosting opportunities in the area because of a relatively cold climate. Based on data collected from the Agricultural Canada Research Station at Onefour, Alberta (less than 50 km to the west), mean minimum temperatures for the month of May have significantly increased in the region since 1965 (Figure 2). This warming trend could explain the presence of red bats in the area because warmer spring night-time temperatures would result in higher prey availability and reduced thermoregulatory costs at a critical time of year when bats are establishing maternity roosting sites prior to parturition. If, as predicted by many global climate change models, summer temperatures continue to increase, the Cypress Hills may become suitable to sustain a population of *L. borealis*. These captures, then, could have implications for predictions about range expansion in other animals as global climate continues to change, especially if *L. borealis* are captured in the Cypress Hills in the future.

Acknowledgments

We are grateful to Ray Poulin and Jeff Lane for comments on the manuscript. We also thank R. Fisher, C. Voss, S. Martinez and J. Adams for help in the field. Erin Bayne, Darren Bender, Ryan Csada, Quinn Fletcher, David Gummer, Kerry Hecker, Matina Kalcounis, Amanda Karst, October Negraeff and Darren Sleep have all collected mistnet data over the past decade. Our research in the Cypress Hills is supported by Mountain Equipment Co-op, Saskatchewan Environment and Resource Management, The University of Regina, and the Natural Sciences and Engineering Research Council of Canada.

Literature Cited

Anthony, E. L. T. 1988. Age determination in bats. Pages 31-46 *in* Ecological and Behavioral Methods for the Study of Bats. *Edited by* T. H. Kunz. Smithsonian Institute Press, Washington, D.C.

Barclay, R. M. R. 1984. Observations on the migration ecology and behaviour of bats at Delta Marsh, Manitoba. Canadian Field-Naturalist 98: 331-336.

Cowan, I. McT., and **C. J. Guiget.** 1965. The mammals of British Columbia. British Columbia Provincial Museum Handbook 11. 414 pages.

Davis, W. H., and **W. Z. Lidicker.** 1956. Winter range of the Red Bat, *Lasiurus borealis*. Journal of Mammalogy 37: 280-281.

Hamilton, R. B., and **D. T. Stalling.** 1972. *Lasiurus borealis* with five young. Journal of Mammalogy 53: 190.

Humphrey, S. R. 1975. Nursery roosts and community diversity of Nearctic bats. Journal of Mammalogy 56: 321-346.

Hutchinson, J. T., and **M. L. Lacki.** 2000. Selection of day roosts by red bats in mixed mesophytic forests. Journal of Wildlife Management 64: 87-94.

Koehler, C. E., and **R. M. R. Barclay.** 2000. Post-natal growth and breeding biology of the Hoary Bat (*Lasiurus cinereus*). Journal of Mammalogy 81: 234-244.

Racey, P. A. 1988. Reproductive assessment in bats. Pages 57-95 *in* Ecological and Behavioral Methods for the Study of Bats. *Edited by* T. H. Kunz. Smithsonian Institution Press, Washington, D.C.

Saskatchewan Environment and Resource Management. 2001. Natural Neighbours: Selected Mammals of Saskatchewan. Canadian Plains Research Centre: Regina, Saskatchewan. 206 pages.

Shump, K. A. Jr., and **A. U. Shump.** 1982. *Lasiurus borealis*. Mammalian Species 183: 1-6.

Van Zyll de Jong. C. G. 1985. Handbook of Canadian Mammals 2: Bats. National Museums of Canada, Ottawa. 212 pages.

Received 17 December 2001
Accepted 4 May 2004

Marsh Rice Rat, *Oryzomys palustris*, Predation on Forster's Tern, *Sterna forsteri*, Eggs in Coastal North Carolina

JOHN H. BRUNJES IV[1] and WM. DAVID WEBSTER

Department of Biological Sciences, University of North Carolina at Wilmington, Wilmington, North Carolina 28403-5915 USA

[1]Current Address: Department of Range Wildlife, and Fisheries Management, Texas Tech University, Box 42125, Lubbock, Texas 79409 USA

Brunjes, John H., and WM. David Webster. 2003. Marsh Rice Rat, *Oryzomys palustris*, predation on Forster's Tern, *Sterna forsteri*, eggs in coastal North Carolina. Canadian Field-Naturalist 117(4): 654-655.

Nesting success of Forster's Terns (*Sterna forsteri*) was examined on two small islands in the Cedar Island area of North Carolina. Forster's Terns laid an average of 2.1 eggs per nest (n = 50) on Chainshot Island and 2.1 eggs per nest (n = 43) on Harbor Island in clutches that consisted of 1 to 3 eggs. On Chainshot Island every egg (n = 107) was lost to predation. On Harbor Island, 72 of 92 eggs were preyed upon. A trapping program, initiated on both islands, yielded 32 Marsh Rice Rats (*Oryzomys palustris*). Stomach contents of 23 rats were inspected, with 92.3% from Chainshot Island and 70% of the stomachs from Harbor Island containing yolk and feathers of Forster's Terns.

Key Words: Forster's Tern, *Sterna forsteri*, Marsh Rice Rat, *Oryzomys palustris*, eggs, nesting success, predation, North Carolina

Reproductive success of Forster's Terns in eastern North America has been poorly documented. In the prairie region of North America (Bergman et al. 1970; McNicholl 1982) and in Texas (Chaney et al. 1978*), most Forster's Tern eggs were lost to wave action and storm damage. In North Carolina, Parnell and Soots (1979*) attributed loss of some eggs to flooding, but they also described an unknown cause of mortality that left large numbers of dead chicks and broken eggs scattered throughout the colony. In subsequent years, continuing loss of eggs and colony abandonment in North Carolina was thought to be due to the effects of flooding (J. Parnell, University of North Carolina at Wilmington, Department of Biological Sciences, Wilmington, North Carolina, personal communication). Although the threat posed by mammalian predators was considered low due to the small size and isolated nature of the islands on which the birds nest, Forster's Terns nesting in the Cape Hatteras National Seashore in 1987 exhibited low reproductive success due to the apparent heavy predation by Marsh Rice Rats (*Oryzomys palustris*) (Cooper 1988*).

Reports of predation on eggs and chicks of Forster's Terns on the east coast of the United States are scarce; however, Marsh Rice Rats have been implicated in the nest destruction of Marsh Wrens (*Cistothorus palustris*) (Kale 1965) and Seaside Sparrows (*Ammodramus maritimus*) (Post 1981). Marsh Rice Rats, the most abundant mammalian denizen of salt-marsh habitats in coastal North Carolina (Webster et al. 1985), prey primarily on animal matter such as small crustaceans (Sharp 1967). We report heavy egg predation by Marsh Rice Rats in two Forster's Tern colonies in the Cedar Island area of coastal North Carolina.

Study Area and Methods

Field work was conducted from 15 May to 30 July 1992 on Chainshot (34°59'N, 76°14'W) and Harbor (34°59'N, 76°13'W) islands, which are located at the junction of Core and Pamlico sounds in North Carolina. Chainshot Island is a small (<1 ha) natural estuarine island dominated by a Smooth Cordgrass (*Spartina alterniflora*) marsh and is located 2.8 km east from mainland Cedar Island. The wrack used as nesting habitat by Forster's Terns was composed exclusively of dead *Spartina alterniflora* that covered the central portion of the island. Harbor Island is a small (1 ha) natural estuarine island consisting of an upland shrub

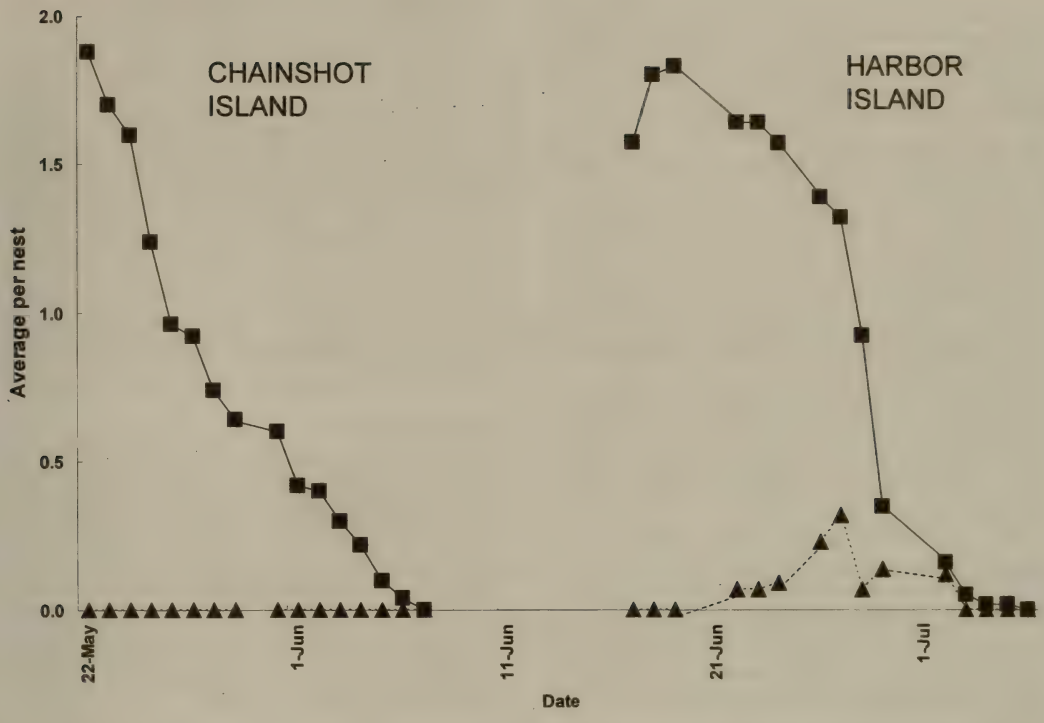


FIGURE 1. Average number of Forster's Tern eggs per nest (squares) and chicks per nest (triangles) throughout the incubation and pre-fledging period at two sites in eastern North Carolina.

thicket and surrounding *Spartina alterniflora* marsh and is located 4.3 km east from mainland Cedar Island. Wrack lines of *Spartina alterniflora* and Eelgrass (*Zostera marina*) were deposited linearly along the edge of the marsh.

An artificial nesting platform (1.5 × 3.7 m) was constructed on Harbor Island in April 1992 in an attempt to improve nesting success by reducing losses due to flooding. The bottom was placed about 0.75 m above the ground and covered with dead vegetative matter similar to naturally occurring wrack on the island; vegetation was pulled through in spots to make it appear as realistic as possible.

On Chainshot Island, fates of eggs in 50 randomly selected Forster's Tern nests (of approximately 100 nests total) were determined during the period between 22 May and 7 June. Nests of 43 Forster's Terns, the total colony, on Harbor Island were monitored during the period between 17 June and 6 July. Nests were identified by mapping positions of nests relative to their placement on the wrack. After allowing several days for initiation of the colony, nest fate was checked in the morning and evenings on each island to determine the relative timing of egg and hatchling loss. All nests were followed to the point of hatching or destruction. Destruction of nests was attributed to predation if evidence of nest predators was present. Nests were usually found abandoned with eggs displaying chewing in the center portion. If predated eggs were not present in the nest, they were usually present on the surrounding wrack or in runways in the surrounding grasses. Eggs that disappeared without evidence of predation were classified as unknown losses. Forster's Terns were the only bird species nesting on either island at the time of this study.

After observing high rates of egg loss, apparently due to Marsh Rice Rat predation, we began a trapping program. Twenty-four Museum Special snap traps were set on Chainshot Island from 22 through 24 June and on Harbor Island from 17 June through 3 July. These traps were scattered irregularly across the wrack used by the nesting Forster's Terns, and baited with peanut butter. Traps were checked twice daily, once just after sunrise and once just before sunset. Captured rats were frozen so that their stomach contents could be examined at the conclusion of the trapping period.

Results

On Chainshot Island, 50 marked Forster's Tern nests contained a total of 107 eggs, with an average

of 2.1 eggs per nest. All but five Forster's Tern eggs were apparently destroyed by predation before hatching (Figure 1). Other egg losses (n=5) were classified as unknown losses. Nests destroyed by predation were abandoned by adults with no attempts to re-nest on Chainshot Island, although these adults, which were not individually marked, may have moved to Harbor Island to renest.

Forty-three nests were marked on Harbor Island, seven of which were on the artificial platform. A total of 92 eggs were laid, with an average of 2.1 eggs per nest. Of the eggs laid, 68 were consumed, 20 hatched, and four were classified as unknown losses (Figure 1). All predation occurred between late afternoon and early morning nest checks. Due to the mobility of hatchlings, it was difficult to monitor their progress, but apparently none survived to fledging as no adults remained on the island long enough to have fledged chicks. None of the eggs laid on the artificial platform survived to hatching.

Thirty-two Marsh Rice Rats were trapped on the two islands, 15 on Chainshot and 17 on Harbor. Densities of the rice rats were estimated at 80 rats/ha on Chainshot Island and 60 rats/ha on Harbor Island using the Hayne (1949) capture-removal method. Marsh Rice Rats were the only mammal captured on either island and all were captured between late afternoon and early morning.

Stomachs of 13 Marsh Rice Rats trapped on Chainshot Island and 10 Marsh Rice Rats from Harbor Island were examined. Twelve of 13 stomachs (92.3%) from Chainshot Island and 7 of 10 stomachs (70.0%) from Harbor Island contained yolk and or feathers. All stomachs contained other plant and animal items.

Discussion

Contrary to what we expected, flooding was not responsible for the loss of any Forster's Tern eggs, despite several days of strong northeast winds that caused high water levels in the Cedar Island area. In this study, predation was the only recognizable form of egg loss. Predation took place nightly with a random pattern of egg loss. Nests of Forster's Terns typically lost one egg at a time, rather than large numbers of eggs being destroyed and stockpiled nightly, a foraging strategy exhibited by introduced European rats (*Rattus* sp.; Austin 1944, 1948).

The Marsh Rice Rat was apparently the only mammal found on Chainshot and Harbor islands, and the stomachs of a majority of the trapped rats contained bird remains. While most eggs were consumed in the nest, a number of eggs were found at the entrances to Marsh Rice Rat runways, suggesting that the nine missing eggs classified as unknown losses could have been carried off by rice rats. The ends of the eggs were removed neatly, and the inside of each egg was polished clean. Avian predators are rarely this neat; they also typically remove the egg from the nest, and are generally diurnal (J. Brunjes, personal observation).

Nesting platforms hold possibilities for future management of Forster's Terns. However, without predator exclusion our platform failed to produce any chicks. The platform could be modified to exclude Marsh Rice Rats by trimming the underlying vegetation, raising the platform slightly, and wrapping slick tin around the legs to hinder the rats' ability to climb into the platform. Our attempt to control predators on Harbor Island, a technique shown to improve nesting success of waterfowl suffering from heavy mammalian predation (Balser et al. 1968; Duebbert and Kantrud 1974; Duebbert and Lokemoen 1980), seemed to slow predation initially, allowing some birds to hatch, but then predation rapidly increased as the rats learned to avoid the traps.

Acknowledgments

This research was supported in part by the National Audubon Society's North Carolina Coastal Island Sanctuary System and The Department of Biological Sciences and the Center for Marine Science Research (Contribution Number 100) of the University of North Carolina at Wilmington. We thank W. Golder and J. Parnell for their valuable assistance and guidance throughout this project. E. G. Bolen, W. B. Ballard, A. J. Erskine, and two anonymous reviewers provided valuable input on the manuscript.

Documents Cited (marked * in text)

Chaney, A. H., B. R. Chapman, J. P. Karges, D. A. Nelson, R. R. Schmidt, and **L. C. Thebeau.** 1978. Use of dredged material islands by colonial waterbirds and wading birds in Texas. Dredged Material Research Program Technical Report d-78-8. U.S. Army Engineer Waterways Experimental Station, Vicksburg, Mississippi. 317 pages.

Cooper, S. 1988. Colonial waterbird studies at Cape Hatteras National Seashore, North Carolina in 1987. Final Report. National Park Service, Cape Hatteras, North Carolina.

Parnell, J. F., and **R. F. Soots, Jr.** 1979. Atlas of colonial waterbirds of North Carolina estuaries. UNC Sea Grant Publication, UNC-SG-78-10, Raleigh, North Carolina. 274 pages.

Literature Cited

Austin, O. L. 1944. The status of Tern Island and the Cape Cod terns in 1943. Bird-Banding 15: 133-139.

Austin, O. L. 1948. Predation by the common rat (*Rattus norvegicus*) in the Cape Cod colonies of nesting terns. Bird-Banding 19: 60-65.

Balser, D. S., H. H. Dill, and **H. K. Nelson.** 1968. Effect of predators on waterfowl nesting success. Journal of Wildlife Management 32: 669-682.

Bergman, R. D., P. Swain, and **M. W. Weller.** 1970. A comparative study of nesting Forster's and Black terns. Wilson Bulletin 82: 435-444.

Duebbert, H. F., and **H. A. Kantrud.** 1974. Upland duck nesting related to land use and predator reduction. Journal of Wildlife Management 38: 257-265.

Duebbert, H. F., and **J. T. Lokemoen.** 1980. High duck nesting success in a predator-reduced environment. Journal of Wildlife Management 44: 428-437.

Hayne, D. W. 1949. Two methods for estimating animal populations. Journal of Mammalogy 30: 399-411.

Kale, H. W. 1965. Ecology and bioenergetics of the long-billed marsh wren *Telmatodytes palustris griseus* (Brewster) in Georgia salt marshes. Occasional Publications of the Nuttall Ornithological Club 5: 1-142.

McNicholl, M. K. 1982. Factors affecting reproductive success of Forster's Terns at Delta Marsh, Manitoba. Colonial Waterbirds 5: 32-38.

Post, W. 1981. The influence of rice rats *Oryzomys palustris* on the habitat use of the seaside sparrow *Ammospiza maritima*. Behavorial Ecology and Sociobiology 9: 35-40.

Sharp, H. F., Jr. 1967. Food ecology of the rice rat, *Oryzomys palustris* (Harlan), in a Georgia salt marsh. Journal of Mammalogy 48: 557-563.

Webster, W. D., J. F. Parnell, and **W. C. Biggs, Jr.** 1985. Mammals of the Carolinas, Virginia, and Maryland. The University of North Carolina Press, Chapel Hill. 255 pages.

Received 24 October 2001
Accepted 17 May 2004

Documenting Pronglorn Antelope, *Antilocapra americana*, in the Peace River Grasslands, Alberta

THERESA A. FERGUSON

Anthropology, Athabasca University, 1 University Drive, Athabasca, Alberta T9S 3A3 Canada
Present address: 10733 150 St. NW, Edmonton, Alberta T5P 1R4 Canada

Ferguson, Theresa A. 2003. Documenting Pronghorn Antelope, *Antilocapra americana*, in the Peace River grasslands. Alberta. Canadian Field-Naturalist 117(4): 657-658.

Fur trade records of the 1800-1855 period document the harvest of antelope in the central Peace River area of northern Alberta.

Key Words: Pronghorn Antelope, *Antilocapra americana*, fur trade, northern Alberta.

Although descriptions of the early historic distribution of Pronghorn Antelope, *Antilocapra americana* Ord, in Alberta restrict them to the south and east portion of the province extending only as far north as 53°N latitude (Mitchell 1980; Soper 1964), fur trade records from the central Peace (56-57°) make sporadic reference to antelope in the 1800-1850 period. See Documents Cited section).

The fur trade posts under consideration here are located in relative proximity.[1] Fort Dunvegan was the longest lived establishment (1805-1918), with several locations, all in the same area as the present day Dunvegan, Alberta (HBCA, PAM, B.56). Fort St. Mary was situated 1818-1820 at the confluence of the Smoky and Peace rivers (HBCA, PAM, B.190). The Hudson's Bay Company post at [Fort Waterloo] Lesser Slave Lake (HBCA, PAM, B.115/a) was located 1815-1933 at the west end of Lesser Slave Lake and its hunting territory extended into the tributaries of the Peace River. The Ile de Campement of Harmon's 1816 diary was situated farther north on the Peace, possibly at the confluence of the Notikewin River (Lamb 1957: 117). Fur trade records do not support the distribution of antelope as far north as Fort Vermilion [Alberta] (HBCA, PAM, B.224); and so few of the Fort St. John [British Columbia] post records have survived, that no particular conclusion can be drawn from the absence of references to antelope in those documents (HBCA, PAM, B. 189).

Antilocapra americana are referred to in these records by different terms: "antelope", "cabri"/"cabrit" and possibly "jumping deer". "Antelope" appeared only in the post-1850 records of Fort Dunvegan. Richardson (1829: 262) speculated that the term, "cabri/cabrit," as used in the Canadian fur trade for antelope, originated from a corruption of the Spanish, *cabra*, or goat. This usage is still found in older English dictionaries (e.g., Webster's 1957). This term appears in the Fort Dunvegan and Lesser Slave Lake post journals and in Harmon's 1816 diary from Ile de Campement. The term, "jumping deer," is found in the Fort St. Mary records of 1819/20 and in the Lesser Slave Lake records of 1819-1821. Whether this use refers to Pronghorn Antelope is not entirely clear. While the term, "jumping deer," was used historically for antelope (e.g., Coues 1965: 634), it is also used for other species, for instance, Mule Deer (*Odocoileus hemionus*), a species which may also have been present in the area of the Peace River under discussion.

The sporadic nature of the historical references to antelope in this area is related to their lack of significance as a provisioning resource in an area where Bison (*Bison bison*) were abundant. Thus, although Harmon described the area around Ile de Campement as rich

[1]Editor's Note: see map in *The National Atlas of Canada*. Fourth Edition (Revised) 1974. Pages 79-80. Posts of the Canadian Fur Trade. MacMillan Company, Toronto.

in "Buffaloe, Moose, Red Deer & Cabri etc.," he did not identify cabri among the species actually hunted to provision the post (Lamb 1957: 117). Other general descriptions of the resources available to the Peace River posts do not mention antelope at all (Lamb 1970; Rich, 1938).

In the Upper Peace, antelope harvests were documented in daily post journals in two periods: pre-1822; and from 1840-1855. In both of these periods, meat provisioning was uncertain and harvesting more opportunistic, but for different reasons. During the early period of competition between the trading companies, posts experienced difficulty in retaining committed Fort Hunters. After 1840, the availability of committed hunters was not a problem, but the depletion of bison and other large game forced the posts to expand their harvest to small game (Ferguson 1993).

Usually only fresh meat was identified by species in the fur trade journals. The main fresh meat hunt occurred over the October-March period. Typical are the following two entries from Fort Dunvegan:

"arrived with 180 lbs of meat of the two cabri killed by Sistey, nearly the half of one was wanting." (HBCA, PAM, B.56/a/10, entry of 14 March 1842)

"hunters after antelope at Bear River" (PAA 74.1, item 122, entry of 16 February 1854).

The last extant Fort Dunvegan journal of the mid-1800s (PAA 74.1, item 122) records the harvest of antelope in 1855, so the population was present until at least that time. The next available source, the District Report of 1885 (HBCA. B56e/1), contains no reference to antelope, nor is there any reference in subsequent materials. It seems likely that hunting pressure after the depletion of the Bison contributed to the extirpation of the antelope in the Upper Peace, but one cannot exclude the possibility that populations persisted beyond the 1850s in areas distant from the posts.

Acknowledgments

I acknowledge the Hudson's Bay Company Archives, Provincial Archives of Manitoba, and the Provincial Archives of Alberta, for permission to quote from the Fort Dunvegan journals. Thanks to three anonymous reviewers for their helpful comments.

Documents Cited

Hudson's Bay Company Archives, Provincial Archives of Manitoba

B. 56	Fort Dunvegan Post records
B. 56/a/10	Fort Dunvegan Post Journal, 1841-2
B. 56/a/11	Fort Dunvegan Post Journal, 1842-3
B. 56/e/1	Fort Dunvegan District Report, 1885
B. 115/a	Lesser Slave Lake Post records
B. 189	Fort St. John Post records
B. 190	Fort St. Mary Post records
B. 224	Fort Vermilion Post records

Provincial Archives of Alberta

74.1, item 122. Fort Dunvegan Post Journal, 1853-5

Literature Cited

Coues, E. 1965. The manuscript journals of Alexander Henry and David Thompson, 1719-1844, Volume 2. Francis P. Harper, New York. 469 pages.

Ferguson, T. A. 1993. Wood Bison and the early fur trade. *In* The Uncovered Past: Roots of Northern Alberta Societies. *Edited by* Patricia A. McCormack and R. Geoffrey Ironside. Circumpolar Research Series Number 3, Canadian Circumpolar Institute, Edmonton. 186 pages.

Lamb, W. K., *Editor.* 1957. Sixteen Years in Indian Country: the Journal of Daniel Williams Harmon, 1800-1816. MacMillan Company of Canada, Toronto. 277 pages.

Lamb, W. K. *Editor.* 1970. The Journals and Letters of Sir Alexander MacKenzie. MacMillan of Canada, Toronto. 551 pages.

Mitchell, G. J. 1980. The pronghorn antelope in Alberta. G. J. Mitchell, Regina, Saskatchewan.

Rich, E. E. *Editor.* 1938. Journal of Occurrences in the Athabasca Department, by George Simpson, 1820 and 1821, and Report. Champlain Society, Toronto, Ontario. 498 pages.

Richardson, J. 1829. Fauna Boreali-americana; or the zoology of the northern parts of British America. J. Murray, London, England. 2 volumes.

Soper, J. D., 1964. The mammals of Alberta. Hamly Press, Edmonton. 402 pages.

Webster New Twentieth Century Dictionary of the English Language. 1957. Second edition. The World Publishing Company, New York. 2129 pages.

Received 17 January 2003
Accepted 6 November 2003

Book Reviews

ZOOLOGY

Birds of Chile

By Alvaro Jaramillo (Illustrated by Peter Burke and David Beadle). 2003. Princeton University Press. 288 pages. U.S. $29.95 Paper, U.S. $55.00 Cloth.

I had several surprises when I began reading *Birds of Chile*. First, the author, Alvaro Jaramillo, was born in Chile, but raised in Canada. The two artists, Peter Burke and David Beadle, are Canadians. So this book is really a Canadian endeavour. The book, as might be expected from the title, covers "all" the birds of Chile (including Easter Island and the section of the Antarctic Peninsular claimed by Chile – and disputed by Britain and Argentina). It also covers the Falkland Islands and South Georgia. The author has his logic for this extension into British (and international) territories. This is not the first Chilean field guide as has been claimed: I know of two English and one Spanish language books.

The book covers 473 species, including 9 endemics. The first question I asked was, is this an accurate coverage? My research found there was no simple answer. I verified that the book did cover 473 species, but this included about 20 species (like Snow Petrel and Emperor Penguin) that are confined to the Antarctic regions and have never occurred in Chile proper. The actual number of species seen in Chile is variously report between 473 and 487 (sometimes 549 is used, however this includes all the subspecies) and the number of endemics is between 9 and 14. My own list is 483 with 14 endemics. The text identifies 9 endemics, not including the Juan Fernandez Firecrown. The problem with the Firecrown entry is that a large chunk of text is missing (due to bad typesetting) and the word endemic is part of the missing text. This would make the endemics list for this book equal 10. I suspect the authors probably did their count electronically for the word "endemic", which would account for their error. More surprisingly, they have not included species like the Juan Fernandez Petrel that nests only on Chile's Alexander Selkirk Island. If they included these island-nesting seabirds the endemic total would reach 14.

Because Chile is a long, narrow country, the author decided to chop the range maps into three and place each part side by side. This novel treatment creates a rectangular map that fits better with the text. While I thought the map innovation was a neat idea it did give some problems. The author's first use of this map format was in a useful section on the eco-geography. A version of the triple-section map has been colour coded to depict the major vegetation zones. The first section, which appears to go from the northern border with Peru to Coquimbo, is shown as total desert backed by high Andean steppe. This is the Atacama Desert and it is the driest part of the world. But it does not correlate with some of the bird distributions. The ranges of several water birds (grebes, duck, herons, etc.) are shown as occupying this desert (in the rivers and along the coast). The second section, which overlaps the first slightly, shows sclerophyllous (Mediterranean-type) forest at the north end (i.e. the south end of the first section). Not only is this incompatible but I think something is amiss with the extent of the colour coding for the desert section. I have been unable to find another eco-zone map for comparison. I also had problems mentally re-aligning the three map sections into one continuous strip. Eventually I photocopied the map and cut and pasted it back into normal format. This helped, but I realized a regular Chilean map is essential to align with the place names given in the text.

When describing the distribution and occurrence of species the author is too generic with those birds that occur in the "peripheral" territories off the Chilean mainland. For example, the Emperor Penguin is rarely seen north of 60° (which includes the "Chilean" section of the Antarctic Peninsular) and this is not clear. Similarly, the Black-faced Finch is rare in Patagonia, but is easily found in the Falklands. This too is not stated.

Having found some problem areas, I hasten to add that this is a very good book for its main purpose. It has good quality, well-organised text accompanied by first-rate artwork. It covers most, if not all of the birds found in Chile. The treatment of species, including new splits, is sane and logical. The book is easy to use and small enough for a back pack (at 21 × 15 cm or about 8 × 6" it does not fit pockets well.) The illustrations cover flying, standing, male, female, juvenile and so forth as appropriate. Given the excellent quality of this artwork the user should have little problem using it in the field. A couple of my plates are rather dark (a problem with quality control of the printing process), but this should not impede their use. I think this book will sell well and this should lead to a second, revised printing.

ROY JOHN

2193 Emard Crescent, Beacon Hill North, Ottawa, Ontario K1J 6K5 Canada

The Birds of Manitoba

Edited by Peter Taylor, illustrated by Rudolf Koes. 2003. Manitoba Avian Research Committee, Manitoba Naturalists Society, 401-63 Albert Street, Winnipeg, Manitoba. 500+ pages. Hard cover $63.95

The Birds of Manitoba is one more of the many regional texts on North American birds, specialized productions that keep getting better. With *The Birds of Manitoba* we have evidence that years of systematic observation by dedicated birders and ornithologists have borne a bounty. The authors of *Birds of Manitoba* have achieved their stated goals of telling you where and when to see the birds of Manitoba, their overall populations, and the likelihood of your having a sighting, and, finally, estimated population trends and distribution patterns. Assumptions are backed up by reams of data collected over twenty plus years; a base from which *Birds of Manitoba* can report authoritatively on the ebb and flow of bird populations as the ecology of Manitoba changes.

The book starts with thumbnail outlines of the province's birding hot spots. They are well written but lacking in those workday details that birders like – concise directions on how to get there. But this is a minor criticism that pales in comparison to other true loves of birders: beautiful bird paintings and wonderful black-and-white sketches. As well as being finely crafted, many of the paintings are educational tools. They enable one to compare similar looking species if confronted by them in the field.

Following the summaries of the hot spots is a more extensive section that provides an overview of the history of ornithology in Manitoba. It outlines the people and the places that make up the ornithological landscape of Manitoba and points to changes in avifauna and their effects on bird populations. *Birds of Manitoba* mentions that Winnipeg anomaly of more House Sparrows reported in that city in the middle of winter than anywhere else in North America.

Other interesting overviews in *Birds of Manitoba* outline the relationships between physical geography and bird distribution, Manitoba ecology and bird habitats, and the effects of manmade changes on bird populations and bird behaviour.

The main body of the text revolves around the species accounts arranged in taxonomical order, an ordering of the bird species by a set of criteria which is now changing because of DNA analysis. These changes have as yet not made a difference in what the birder sees with the naked eye only to what the ornithologist notes in the laboratory.

The species accounts of the 382 birds known to occur in Manitoba start at Loons and end at Old World Sparrows. The best known representative of the Old World Sparrow family is the House Sparrow. It is deftly dealt with. A concise description of what it looks like is followed by a jaundiced history of this bird in North America. It is seen as a pest by *Birds of Manitoba*. However, it is not seen as declining in Manitoba as it is suspected to be in other jurisdictions.

One of the pressures on the House Sparrow is the expansion of the House Finch from the east coast inland, a factor that is noted in the species account on House Finch in *Birds of Manitoba*. Another avian pressure on the House Sparrow is the southern expansion of another species, not a competitor for nesting sites, but a predator – the Merlin. As with the House Finch, the chronicle of the Merlin in *Birds of Manitoba* points out that the Merlin's expansion requires even better documentation to properly determine its population numbers province wide. *Birds of Manitoba* mentions that Merlins do not normally make their own nesting sites but depend on abandoned crow or magpie nests. So the web that may ultimately affect House Sparrow numbers must encompass the corvid family.

The word sketch of the American Crow provides more information which one can use to speculate on the future of the House Sparrow in urban Manitoba. In this case, the authors sense that the Breeding Bird Surveys which point to a long-term decrease in crow population go against what other observers find. So while it is not the stated intention of *Birds of Manitoba* to document the interlocking relationships between bird species, you can use this book to do so.

Similarly, *Birds of Manitoba* is not a field guide. Nevertheless, it has a number of little gems of explanation. The description of what to look for if you ever happen upon a Scissor-tailed Flycatcher is priceless.

As a birder I have grown used to identifying birds by their jizz, that gestalt of shape, form and telltale behaviour patterns of each different species of bird. *Birds of Manitoba* has a jizz. Its style hearkens back to the writing of Bent and the paintings of Audubon, times when observational skills were a joy to gain and respected for their own sake.

MARTIN BAILEY

102-1833 Coteau Avenue, Weyburn, Saskatchewan S4H 2X3 Canada

Built for Speed: A Year in the Life of Pronghorn

By John A. Byers. 2003. Harvard University Press, Cambridge, Massachusetts. 230 pages. U.S. $24.95 Cloth.

This is not a book about NASCAR racing cars. Rather, as Preface author Rick Bass writes, "[This] is the kind of work for which I have the greatest respect: watching one animal for hours each day, days upon end ... regardless of the conditions." Indeed, author Byers began his continuing intensive observations of pronghorns on the National Bison Range (NBR), in the Flathead Valley of western Montana, in 1981. Although established primarily to save the bison from the brink of extinction, the NBR inadvertently was important to the salvation of the pronghorn, perhaps the most charismatic of big game animals inhabiting the American Great Plains.

Author Byers explains that an objective in writing his book "is to convey both my intellectual and my aesthetic appreciation of the species", clearly one that continued to amaze and delight him. Also he hopes to convey an impression of what it is like to conduct a long-term field research project in North America, largely focused on a single species.

Modest in size, 5¾ (147 cm) × 7¼ (185 cm) × 1" (2.5 cm), the book contains much information about the behavior and social organization of this unique ungulate, so renowned for its speed, endurance, and eyesight. Thirteen chapters intimately describe the year-round activity of the pronghorn, especially its individual and group behavior in relation to biological processes and ecology.

The book is written in a very readable, semi-popular style, supported by chapter-end notes, literature citations, and intimate photographs. Byers is unusually gifted in sharing the beauty and wonder of the pronghorn and its ecology with his readers.

His behavioral and social studies of pronghorns are largely about individuals and groups, made possible by ear-tagging fawns or by recognizing subtle morphological differences among individuals. In this manner, Byers and his students were able to follow the fortunes and fates of individuals such as GY (green tag in the right ear, yellow tag in the left) or BUG (a female that had a small spot of black hair, resembling a bug, on her nose). Their studies clearly show that the social ranking and dominance of pronghorns, males and females alike, is established early in life according to birth sequence.

Byers sometimes thinks and writes a bit outside the conventional biological box. He colorfully describes the pronghorn body as having a "four-chopsticks-in-a-bratwurst" appearance. Noting that a running antelope can attain a speed of 60 mph by strides of 29 feet, this rate translates into covering the length of a football field in 3 ½ seconds with slightly over 10 strides. He tells that the comparably rapid growth of pronghorn young is attributable to the energy content of the nursing mother's milk, which is about twice that of cow's milk and 2.5 times that of human milk.

We further learn, for example, that the 30-square mile NBR supports about 258 tons of bison, 44 tons of elk, 17 tons of white-tailed and mule deer, 8 tons of mountain goats, and 5 tons of pronghorn, and that the grasshopper biomass of 412 tons, or about 120 percent the tonnage of big herbivorous mammals.

Unfortunately the author often fails to give times and dates of his many interesting observations. Indeed I was left with many questions. For example, he intimately describes the birth of one fawn but then fails to describe that of its twin. While the entire refuge is fenced, are the pronghorns he studied totally contained within it year-round as are the bison? Is the pronghorn population cropped annually by trapping and removal, again as are the bison? How do pronghorn population numbers fluctuate from year to year, and in response to what cause?

Further, how do Byers' interesting observations of individuals and their behavior relate to or influence the overall pronghorn population of about 120 on the NBR? Perhaps such basic concerns are beyond the rather narrowly stated scope of research reported upon in this one work, and may be addressed in one or more of his seven cited publications, and particularly in his monographic *American Pronghorn: Social Adaptations and the Ghosts of Predators Past* (University of Chicago Press, 1997).

With his emphasis on individual and group behavior, it seems puzzling why he does not credit David W. Kitchen's work *The Social Behavior and Ecology of the Pronghorn* (unpublished Ph.D. dissertation, University of Michigan, 1972) also undertaken on the NBR. Byers similarly overlooks R. E. Autenreith and E. Fichter's study, *On the Behavior and Socialization of Pronghorn Fawns* (Wildlife Monographs 42. 1975) as well as Arthur S. Einarsen's pioneering monograph, *The Pronghorn Antelope* (Wildlife Management Institute, 1948), all of which contain much behavioral information.

While I found *Built for Speed* interesting and informative reading insofar as individual and small groups of pronghorns are concerned, it is likely to be disappointing to those having a broader interest in pronghorns, particularly in their population dynamics and management.

HENRY M. REEVES

22250 Boulder Crest Lane SE, Amity, Oregon 97101 USA

Coral Reef Fishes: Indo-Pacific and Caribbean – Revised Edition

By E. Lieske and R. Myers. 2002. Princeton University Press, 41 William Street, Princeton, New Jersey. 400 pages. U.S. $24.95.

The vast geographical range of the globe's coral reefs and the diversity of their fish species prove challenging for writers of field guides. Nevertheless, Ewald Lieske and Robert Myers have produced not only an excellent guide to reef fishes of the Indo-Pacific and Caribbean, but also a book that is comprehensive and well organized into a single compact volume.

The guide consists of an introduction, colour plates and descriptions of species, and indexes. The introduction defines the book's application and teaches a mini biology lesson. It educates the reader about the structure and ecology of the coral reef environment, and touches on adaptations and mechanisms employed by fish for survival. The section dealing with conservation of reef fishes was pleasing to see. However, to further impress the global responsibility for marine conservation upon all, from the average tourist to the exploitive industries, I would like future editions to include the effects of global warming on the marine environment. Everyone has a role to play in reducing greenhouse gas emissions as they negatively impact upon the Great Ocean Conveyor (also called the thermohaline circulation) that in turn risks causing catastrophic effects on both global climate and sensitive marine ecosystems.

This guidebook achieves the amazing feat of covering more than two thousand species in one small book, providing excellent coverage of the Indo-Pacific and good coverage for the Caribbean. Although the book includes most species a reef visitor could encounter, it is not all-inclusive. For instance, there are over 400 documented species of sharks worldwide, including oceanic varieties. Requiem sharks alone account for 48 species that dominate the tropical shark fauna. This book describes only 32 species of sharks, of which 13 are requiem sharks. However, those described are common shark species found in the Indo-Pacific and Caribbean that either live or spend part of their time in the reef environment.

This guidebook is separated into two sections, one for the Indo-Pacific and the other for the Caribbean. Species within each section are grouped by family. There are also two valuable indexes at the end of the book, one of scientific names and the second of common names.

The provision of the scientific (Latin) names as well as common names facilitates the book's use by amateurs and professionals alike. However, the danger with using common names is that they may differ from region to region. Nomenclature is also not without controversy, sometimes resulting in the splintering of species or classification of new species. However, in this guide, species identification is quite up-to-date and accurate.

The sketched illustrations are clear and detailed and sometimes include plates of juveniles. They are remarkably accurate, capturing the animal's true colours as seen in their particular underwater habitat. Handy pointers identifying key physical characteristics also help with quick species identification, although I feel they could be more distinct. Descriptions of each species are brief but concise. Size and physical descriptions (for both sexes where applicable) are provided, as well as their ecology, distinctive behaviours, concentrations and range.

The only major flaw in this revised edition is the omission of maps. References on pages six and seven erroneously refer the reader to maps of zoogeographical regions on the inside front and back covers. Maps are needed for readers to appreciate the descriptions of these regions in the introduction. More importantly, they are absolutely vital for confirming a species' range according to the descriptions provided throughout the guide.

Likely its most valuable feature, this book's small size allows for it to be carried from one dive site to another and easily transported in luggage. However, its pages are not waterproof. If used on-site, it could be easily water-damaged. So it should be protected from the elements and left aboard ship for pre- and post-dive referencing.

SUSAN CADORETTE

1541 Scottanne Street, Greely, Ontario K4P 1G8 Canada

Grizzly Heart: Living Without Fear Among the Brown Bears of Kamchatka

By C. Russell and M. Enns. 2003. Random Hoe Publisher. 357 pages. $24 Paperback.

This book is a sensation. It will change how we view wildlife, and it will affect management and conservation of large wildlife in revolutionary terms. The book is also sensational since it is written by non-scientists, a naturalist and an artist, with a life-long interest and devotion to wildlife revolutionizing narrow scientific tunnel views. Embarrassing enough for the "free" western wildlife research world, the authors had to go as far as Kamchatka in Russian Far East to implement their view that large mammals such as Grizzly Bears are not a major threat to humans. Instead, all over the world humans threaten wildlife. Why was this work carried out in Kamchatka? Simply, because all over North America and elsewhere, the experiment of the authors was not really given a chance, neither funded nor allowed to be carried out. For

instance, in North America, it is widely implemented by governmental agencies research scientists. The public believe that large predator mammals like Grizzly Bears are generally dangerous to humans; thus, they need to be controlled. This is why hunting bears is still widely accepted and why hunting predators is seen as "heroic" by the general public. However, as the authors show so impressively, Grizzly Bears can be petted and they can live well in proximity to humans, if they are treated and respected correctly. The authors show in their book that this claim is well backed up by historical facts on how Russian natives lived together with bears for over thousands of years.

Despite the well-accepted work by many zoos and circuses, by Konrad Lorenz (raising geese and ravens), J. Goodall and B. Galdikas (raising monkeys), B. Kilham and Ed Gray (raising Black Bear orphans), Terry D. DeBruyn (living closely with bears) and others, and mostly to cater to the powerful hunting (resource) lobby, this aspect of wild bear biology brought forward by the authors was never really considered, nor really allowed in classical wildlife management circles. It was an outstanding achievement of the Canadian authors to go to Russia as early as 1996; only few other western people acknowledged the opening political situation and had the vision to work and to publish in an area as remote and hidden as Kamchatka (see for instance the work by Emma Wilson and also by Ullrich Wannhoff). Using their own small plane to overcome transportation problems in remote Kamchatka is another outstanding aspect of this book. The real punch line comes when the authors basically stole three orphaned bear cubs from a local zoo and hand-raised them in a remote nature reserve, showing that such "predatory" animals can do well among humans and adjust back to nature easily.

Obviously, anti-poaching action, bear-talk and some Russian realities are other interesting themes of this book. As a reader, I am curious to see the paintings by M. Enns, which are so often mentioned in the text but not part of this publication. The fact that Russia allowed the authors to carry out their experiment over several years shows how wrong an opinionated Western World can be in its attitude and science: strict and narrow views are usually misleading, and instead, an open-minded diversity of approaches is required to study wildlife in a more meaningful way. For additional project information see the authors' website http:// www.cloudline.org/.

FALK HUETTMANN

Institute of Arctic Biology, Biology and Wildlife Department, University of Alaska, Fairbanks, Alaska 99775-7000A USA

Handbook of Birds of the World. Volume 8: Broadbills to Tapaculos

Edited by Josep del Hoyo, Andrew Elliott, and Jordi Sargatal 2003. Lynx Edicions, Barcelona, Spain. 850 pages. U.S. $195. Cloth.

This volume of the *Handbook of Birds of the World* covers Broadbills, Asities, Pittas, Ovenbirds, Woodcreepers, Typical Antbirds, Ground-antbirds, Gnateaters, and Tapaculos; in all just over 670 species. These include some of the world's most wildly coloured birds, the pitas, and some of the most uniform little brown birds such as the horneros. Like its predecessors this volume has great photographs and artwork, current distribution maps and comprehensive text. The editors are continuing to maintain their uniform, high standard.

With this volume the Birds of the World project has turned more than one corner. First, it is halfway through its allotted task, having covered slightly over half of the approximately 200 families of birds in the world. Second, it has finally reached the passerines. This is the last order of birds out of about 30 orders, and this will fill the remaining volumes. It includes close to half the known species. The biggest change is in the nature of the birds themselves. In the past it has dealt with birds that are relatively well known. For example, a lovely drawing of the Northern Pintail (*Anas acuta* in volume 1) can be found in Nebumum's Egyptian tomb from 3500 years ago. It is a widespread and uniform species (there are only two tiny populations of subspecies on remote islands) and has lived close to developed nations for millennia. The tapaculos, by contrast, live in remote jungles that are rarely visited by scientists or even informed travelers. They are frustratingly hard to observe and often difficult to identify. While the indigenous folks know their home turf, they have never applied the scientific discipline needed to separate subspecies or closely related species.

With this in mind I have been keenly aware that this volume represents the contemporary "bible." I looked carefully at the current state of taxonomy compared to the species accounts. While I think this volume is current I did find several points of confusion. First there is no great consistency in the English names, or even in the alternative names. Second, the splits (for in tropical small bird biology this is the trend) made pre-1997 are included. Post-1997 the record is less clear. I took a sampling of 50 species and found that the English name and scientific names were consistent with other published literature for over three quarters of the species. About 15% the birds were given as sub-species, rather than full species. For the remaining birds there were more significant differences. This is not a criticism of the *Handbook of Birds of the World* as much as comment on the state of the knowledge of taxonomy for species that typically live only in some Amazonian backwater or on top of a remote mountain. A good example of these problems is shown by the Orange-bellied Antwren (*Terenura sicki*) that is also known as the Alagoas Antwren. This volume of

the *Handbook of Birds of the World* lists a completely separate species with the same name, the Alagoas Antwren (*Myrmoherula snowi*).

I did a less intensive check of the notorious woodcreepers and did not find any taxonomic problems. I did note that the authors had split the Buff-throated Woodcreeper (primarily Brazil) to give the Cocoa Woodcreeper (Costa Rica and north). I have been adding notes on specific details to my Birds of Costa Rica (*A Guide to the Birds of Costa Rica*, by F. Gary Stiles and Alexander F. Skutch, Cornell University Press, 1989) to verify during my visit to that country in February 2004.

Another important difference between this volume and the others is that the authors have used a far higher proportion of unpublished material. Despite the lack of a formal peer review, I am sure the authors were judicious in the selection of material. Such unpublished data are identified in the text.

Handbook of Birds of the World Volume 8 opens with an essay on the history of bird classification by Murray Bruce. This provides a useful background to the taxonomic difficulties that will follow with the passerines. In places the text is somewhat dry and biblical in that it moves from one master to student after another, but this is part of the process of understanding the history of taxonomy.

The quality of the artwork is consistent with the other volumes. I did my usual scan for errors and could find none. The almost 500 colour photographs are quite remarkable. The quality is similar to other volumes. We need, however, to remember it is easy to photograph a large, unafraid Blue-footed Booby (*Sula nebouxii*), but it is a real challenge to achieve the same quality with skulking understory birds. Any one who has visited the rainforest will know how hard it can be to see these birds clearly for more than a few seconds. There is one photograph of a Scalloped Antbird (*Myrmeciza ruficauda*) that exemplifies these problems. The bird is barely visible; only its round eye and the fact it is likely in the centre of the photograph gives it away. Another innovation is the English names in the photograph captions are now in bold font, making them much easier to find. A typical photo caption is one to two paragraphs long and I found the English name was difficult to pick out when scanning for a particular species in previous editions.

The range maps are similar to previous editions with one important change. These maps now include the major rivers. Thus it is much easier to judge a bird's range. For example, it is easy to pick out the Rios Napo, Negro and Salimoes as Amazon tributaries, which in turn allows the reader to estimate the position of Belem, Manaus and the Ecuadorian border. The book ends with about 4000 bibliographical references that include some text changes to make them easier to use.

ROY JOHN

2193 Emard Crescent, Beacon Hill North, Ottawa, Ontario K1J 6K5 Canada

Important Bird Areas in Africa and Associated Islands: Priority Sites for Conservation

By L. D. C. Fishpool, and M. I. Evans. 2001. Newbury and Cambridge, UK. Pisces Publications and BirdLife International (BirdLife Conservation Series Number 11).

This publication is by no means a booklet. While I was reading it during connecting flights from Seattle to Vancouver, the U.S. customs officer asked me whether I stole the local phone book. Instead, this book presents the major large-scale conservation data source for African birds and their habitats. It's the first and urgently needed consistent data collection of its kind for Africa. Therefore, the authors presented a milestone publication of international importance for global biodiversity and conservation management.

The Important Bird Area (IBA) concept is already well established, and carried out world-wide. This book deals in 1144 pages with descriptions of 1228 IBAs in 68 African countries and associated islands. Approximately 100 authors contributed to this unique publication, most of them with an English or anglophone background. This cultural bias is obvious throughout the entire book. For instance, the countries with the longest text sections, the best information, and with most of the IBAs, are usually the ones with a European, and specifically British, colonial history: Kenya, Tanzania, Ethiopia, Madagascar and South Africa. Yes, it's true that countries with the highest biodiversity usually carry the richest natural resources and therefore, historically attracted European countries. However, less than 3% of the cited literature comes from African contributors, confirming the anglophone bias in African avian investigations and conservation. From a truly "global village" perspective and treating its citizens fairly and equally, African readers might be concerned. Summaries in Swahili, French, Portuguese or in any other language are not provided either.

The data collection and IBA process is well described in this book. Four data sources were used to derive the IBAs for all of Africa: information from *Birds to Watch 2*, The BirdLife Biodiversity Project, atlases of Afrotropical bird distributions, and Wetlands International data. Many international conservation agencies contributed as well, but I am not sure if all the information and publications on Africa available world-wide were used, e.g. Russian ones. The book has 30 descriptive photos of African biomes; 2313 species of birds are covered (referred to by their scientific names) and their population estimates are provided. Readers interested in seabirds will like the great

information provided for these species in the African island chapters. It is commendable that relevant mammals, reptiles and amphibians are also considered by the authors. Ten very detailed appendices complete the book. The African IBA program started as late as 1993, and knowing African and international working conditions the authors have to be congratulated and highly respected for their achievements and skills related to African (bird) conservation.

The outlined IBAs link well with the major international agreements and conservation programs such as CBD (Convention on Biological Diversity), RAMSAR, WHC (World Heritage Convention), CMS (Bonn Convention), AEWA (Agreement on the Conservation of African-Eurasian Migratory Waterbirds), CITES (Convention on the International Trade of Endangered Species), UNCCD (United Nation's Conventions to Combat Desertification), UNFCCC (United Nations Framework Convention on Climate Change) and UNESCO's Man and the Biosphere Program. One hopes they will make a difference.

For this major publication, BirdLife International was supported by the Royal Society for the Protection of Birds (RSPB), Global Environmental Facility (GEF), United Nations Development Program (UNDP), Pisces Publications and others. Considering the magnitude of these global agencies and their believed expertise, some topics in this publication are remarkable and should be further addressed here. For instance, the statement in this book that IBAs are generally connecting the important sites and that they present a network remains open for discussion. Not all African birds covered in this publication will be found in social aggregations, as assumed for the RAMSAR convention (after which concept the IBAs are designed). Another serious flaw could lie in the representativeness of IBA locations. Birds and IBAs can only be meaningful indicators (as claimed in this book) when they come from a sampling regime representative in time and space. Usually, IBAs were not derived from such a sound and spatial research design, but instead established from queries, existing data and traditional or local knowledge on where most birds would be located throughout seasons. For a large continent like Africa with inadequate infrastructure, this information might be biased by human access or other factors constraining equal survey effort. Do IBAs present nothing but a "land grab"? The least one can say is that these IBAs don't acknowledge directly bird migration corridors, as commonly implemented in other continents for avian conservation management. In the methods chapter of this book, BirdLife makes clear that convenience, but not scientific input, played a major role for African IBA delineations; there is no plan to include research in future actions! Science-based decision-making, the major paradigm in other parts of the world, seems to be left out when it comes to African IBAs. Much science is still needed, e.g. to assess bird turnover rates in important IBAs covering at least 1% of global species populations. In the absence of any other and existing African bird conservation exercises, we have to use these IBAs and perceive them as a world-class achievement. The African IBAs are part of the IBA and World Bird Database (WBD); however, much more could be done with these data to stimulate a digital and web-based infrastructure and data provision for decision-making and for the scientific community world-wide on topics related to Africa.

BirdLife bases its work on Community-based Conservation (CBC): "This encompasses the principles that conservation cannot and should not be pursued against the interest and wishes of local people…". "…it is self-evident that conservation action on the ground will only be stainable in the long-term if it is undertaken with and by the people living in and around the high-biodiversity areas". This statement, the ultimate BirdLife paradigm, baldly ignores what sustainability originally means ("don't use more than what re-grows") and is easily proven wrong by the huge number of sad examples world-wide where sustainability of resources was not achieved: yes, a local human population can overharvest a natural resource indeed. It might well be that this so-called democratic and sustainable CBC policy is the major reason why agency conservation so far has failed to save global biodiversity and is achieving less than what is possible and what should be done; it harms global biodiversity and humans alike. Prospects for the global biodiversity future are known to be dim.

While nature gets lost at an incredible speed worldwide, we happen to write ever bigger and better books on these very last leftovers. The human misery in Africa alone appears to be overwhelming and almost unsolvable, this books deals with avian aspects though. Africa is a conservation paradox heavily reflecting the global situation and globalization. Unfortunately, BirdLife spares less than a page in this book on this crucial topic.

Only high quality data convince the public and in political conservation discussions. In these regards the book is weak for two reasons: presented data are not always highest quality, and Africa's situation is getting worse every day, definitely beyond the publication of this book. Bird research, and certainly birding, has not halted the African conservation chaos, yet.

I think all these things need to be known when interpreting African IBAs for biodiversity and conservation management. This book remains a unique, and the best available, large-scale data compilation for Africa's avian and habitat conservation. It is hoped that this book and the global situation will allow Africa and its resources to be saved; ignoring America and the rest of the world though in this context might prove fatal for this continent and its (avian) biodiversity.

FALK HUETTMANN

Biology and Wildlife Department, Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775-7000A USA

Snakes of the United States and Canada: Natural History and Care in Captivity

By John Rossi and Roxanne Rossi. 2003. Krieger Publishing Company, Florida. xxxvi + 520 pages. U.S. $145.

This substantial hardcover builds on the Rossis' previous two-volume set on the captive care of snakes, published in 1995. The authors have revised some information based on new data and have also expanded the scope of the book to include basic information on the natural history of each species, resulting in a single authoritative volume covering all currently recognised species within the continental United States and Canada. The price of this book, combined with its ambitious scope, may deter novice or casual herpetoculturalists and herpetologists from adding it to their collections; however, its well-written, accessible style and wealth of "hands-on" experience make it a valuable resource for anyone with an interest in our native North American snakes.

Dr. John Rossi is a veterinarian specialising in the care of small animals and "exotics," with a particular interest in herpetofauna. His wife Roxanne is an experienced curator, whose first-hand knowledge is evident throughout the discussions on captive care. Together, the Rossis have kept over 90 of the native species discussed in the book, and have published numerous articles and books based on their observations. They have also undertaken extensive research and consultation with other experienced keepers, as evidenced by the impressive list of acknowledgments and the 21-page bibliography. The result is a thorough reference document, which nonetheless recognises (and promotes) the need for additional investigation into certain less well-known species.

The Rossis' passion for their topic is evident throughout the volume, beginning with the introduction and overview of the natural history of snakes. Their position on captive care as a source of valuable information and understanding, which could assist conservation efforts, is a recurring theme within the book. A short chapter on conservation is included in the introductory section of the book, which touches on the issues of habitat loss and fragmentation, road kills, pollution and human attitudes towards snakes (fear and loathing vs. overzealous collecting by hobbyists and traders).

Part 1 of the main body of the text deals with general care information for the keeping of snakes. Housing is the first subject dealt with, based on the reasoning that prior to obtaining any snake, the owner should first have a suitable home ready for it. Various types of housing set-ups are described in detail, along with colour photographs and a summary table of suitable enclosure sizes (based on standard aquarium sizes). This section also covers the other basic components of captive care, from selecting, obtaining and transporting the chosen snake, to keeping, handling, feeding and breeding it. The discussion on reproduction includes methods of sexing the snake, tips for successful breeding, and instructions on rearing neonates. A summary table presents information on breeding season, clutch size and incubation period for the various species. The Rossis emphasize the importance of keeping accurate records, both to the individual keeper and to herpetology as a whole when these records are published. They also discuss the circumstances under which a captive snake should or should not be released back into the wild.

The individual species accounts are presented in two parts. Part 2 describes the nonvenomous snakes (including inoffensive rear-fanged species such as hognose snakes, night snakes, etc.) while Part 3 deals with the venomous snakes. These sections are arranged alphabetically by scientific name; for ease of reference, the book also includes an annotated list of genera preceding Part 1, and an Appendix listing accepted common names and their associated scientific binomial. Part 3 is prefaced with a brief cautionary introduction to the essential differences in technique required when keeping, transporting and maintaining venomous species. Each species account provides a brief summary of reported information on distribution, habitat, physical characteristics, prey and predators, and reproduction in the wild, accompanied by a range map (primarily continental United States/southern Canada, adjusted as necessary for wide-ranging species like Common Garter). This discussion on natural history is followed by captive care information including tips from the Rossis' experience on preferred housing, food, and other requirements. Notes on potential feeding or health problems are also included. Superb colour photographs enhance each species account.

A summary of the species' basic needs and Maintenance Difficulty Index (MDI) is also included in each species account for quick reference and comparison between species. The MDI indicates a species' relative difficulty level, based on the authors' experience. A rating of 1 is applied to species suitable for novices, such as the hugely popular Corn Snake. More challenging species may have highly specific habitat requirements or hard-to-obtain food preferences. The most difficult species are rated as having an MDI of 5. The explanation of the MDI is somewhat difficult to find within the discussion on choosing a species in Part 1 (a sample species information summary, with explanations of the types of data presented therein, might have made a good addition to the book). However, this minor difficulty is offset by the inclusion of a reminder of the ranking system (1 = easiest, 5 = most difficult) in each species' information summary. Other information included in the summary is the species name, average adult length, appropriate food items, cage size, substrate, heat and light sources, temperature range (in Celsius and Fahrenheit), and special considerations such as any potential health issues to watch for.

In conclusion, *Snakes of the United States and Canada* is an impressive compilation of natural history and captive care data for our native North American species. For those readers interested in supplementing their collection of field guides or species care handbooks, this book is a worthwhile acquisition. Furthermore, anyone considering snake ownership would be well advised to at least borrow a copy.

AMY MACPHERSON

2781 Lancaster Road, Suite 200, Ottawa, Ontario K1B 1A7 Canada

Stonechats: A Guide to the Genus *Saxicola*

By E. Urquhart and A. Bowley. 2002. Yale University Press, New Haven and London. 320 pages. U.S. $60. Cloth.

This book is delightful and does the *Saxicola* genus a great service. It covers 14 members of this genus from the Old World, which is as fascinating as it can get for birders since it deals with countries like India, Nepal, Russia, Indonesia and with various other fascinating locations in Europe and Africa.

Obviously, this book is a great reflection of the so entrenched English and European birding culture, and the author links also well to Russian, German and Scandinavian *Saxicola* studies. The explicit goal of this book is to provide as much information on the Stonechat species as possible. The authors achieved in their book a huge compilation of a tremendous amount of information and references relevant to Stonechats such as Nest Record Cards from the British Trust for Ornithology (BTO), BTO Migration Atlas, World Bird Database by BirdLife International, 10 museum collections and many others; for instance, over 173 individual investigators are mentioned in the acknowledgment section of this publication. This makes for a text crowded with details.

The very detailed accounts for the 14 species and their subspecies deal with taxonomy, identification, description, distribution, breeding, habitat, voice, food, movements, behaviour, moult, conservation and literature references.

From a biologist's perspective, some of the presented distribution maps might have too many straight lines, but they show great detail in regards to extralimital sightings, wintering, summer and subspecies distributional ranges (but not search effort and migration flyways). The limitations of these maps are also well addressed and explained. For people with an interest in avian biogeography, this book presents a large goldmine consisting of fascinating endemism and distribution data, e.g. for White-tailed Stonechat and Pied Bushchat. The text and presented data offer great opportunities for further spatial interpretation and predictive modeling. A comprehensive World Distribution Map for the genus *Saxicola* is unfortunately missing.

Tables showing wing, tail and bill measurements are also presented but some do not provide sample sizes. The voice sections and sonograms are nice summaries on what is known on the vocalization for each species. Often, the presented vocalization data cast serious doubt on the traditional concept of point count surveys and habitat mapping for these species since they can sing during migration even, and also mimic other species brilliantly; often also both genders can sing! The authors' concept that only birders would decide which exact bird names are used eventually for bird species world-wide might still be open for discussion. Anyway, it's great to read the section provided on explanations of English and scientific names.

Remarkable are the extremely powerful and very well done colour plates and the many smaller fascinating black-and-white sketches displaying specific behaviours. They are based on great field observations by A. Bowley and E. Urquhart. Over 100 photographs are provided as well allowing for excellent visual aids in species identification.

For my taste, some of the interpretations of the reported research findings are too nationalistic, e.g. stating that birds in Germany, in the former USSR, in Greece, in UK etc. would do specific things. Besides presenting a generalization, such an interpretation does not consider that the area size differs so much among countries. Instead, it might be better to state findings from a sample of a population or from studied individuals.

The authors say that "...many younger birders now only concentrate on identifying and seeing as many different species as possible, without taking time to study the all-round ecology of the species they see". The book includes a short but informative *Saxicola* DNA chapter by Wink et al. dealing with long lists of TCAs, RAAs, CGAs etc. which I cannot fully comprehend; hopefully the birder in the field can. The authors suggest to split the Common Stonechat complex into three species. Generally, one finds birders and geneticists closely linked nowadays, but for me they represent odd bed-fellows. Geneticists dictate a lot of what happens in the birding field nowadays. However, so far avian geneticists have not always clarified situations but rather made amateur birders more dizzy in what constitutes a species, a subspecies and who is evolutionarily related to whom.

This book includes 11 pages of international Stonechat literature references. This provides for a text which offers much fascinating reading such as for instance for the Stolizka's Bushchat and for the highly endangered Hodgson's Bushchat. Interestingly enough, albinism occurs in the genus *Saxicola* whereas leucism appears to be non-existent in the literature and is probably very rare. Presented conservation topics in this book deal for instance with the stability or decline of national *Saxicola* populations, but caution is to be

used since many population estimation methods differ greatly by country and in the time-windows for which these data are presented. As for many birders from central and northern Europe, the authors elaborate on the believed to be very detrimental effects of (song) bird hunting in the southern EU (but they show less attention for these issues in Africa). A consistent theme is that landscape changes affect all stonechat species; their relations with forthcoming climate change are not elaborated on.

True preferences for nest, food and habitat, taking their availability fully into account, are still not reported and are usually not known for most of the discussed species. This presents often a shortcoming in traditional birding books (the difference between resource use and resource preference has been known for over 30 years and should really be addressed in modern book texts).

As this and other advanced birding books show, the birding, taxonomy and publishing world has just not found a convenient way to describe and summarize relevant species plumage identification features; e.g., in a table or in any other format easy to comprehend for the user. Instead, the descriptive plumage text still deals with all the "usually", "oftens", "manys" and other sometimes vague terminology trying to put (individual) feathers and colours into words; over decades, this has developed into a slang of its own, presenting almost an anthropological literature phenomenon. Here two such examples from the text: "The lower mandible is pale horn-brown on the basal third", and "Underparts are also duller than in the adult female and the breast and foreflanks can show narrow brown fringes to the feathers giving a slight mottled appearance".

Anyway, this publication makes for the stonechat bible, presented by the authors as a true labour of love and obsession; they are to be congratulated. This publication is worth reading, and should stand in your bookshelf for specifics on species information and identification.

FALK HUETTMANN

Institute of Arctic Biology, Biology and Wildlife Department, University of Alaska, Fairbanks, Alaska 99775-7000A USA

Birds of Yorkton – Duck Mountain

By C. S. Houston and W. Anaka. 2003. Saskatchewan Natural History Society, 206-1860 Lorne Street, Regina, Saskatchewan S4P 2L7 Canada. ii + 318 pages. Paper $20 plus $4 shipping.

In Saskatoon there is a powerhouse of a human called Stuart Houston. As a professor of medicine he has influenced many young lives, not the least his own children. From a tender age he had a passion for birds, and I do not mean as a birder but as a scientist. This passion has resulted in a lifetime of bird banding, research and many publications. This alone would make his achievements remarkable. He has another achievement to his credit. He has encouraged, led or cajoled an army of people to join in his passion. There are a large number of people who now band, write, research, observe and record, myself included, as we never did before. For *Birds of Yorkton-Duck Mountain* he is joined by a Yorkton local, Bill Anaka.

Birds of Yorkton-Duck Mountain is a very thoroughly researched collection of all the available data on the birds in this corner of Saskatchewan. Anaka and Houston have combed all conceivable pockets of information from Audubon notes to unpublished data. The species account gives a very clear picture of the status of all birds recorded from Quill Lake to the Manitoba border near Shellmouth. These accounts cover common nesters to bizarre and clearly incorrect reports. They are well presented and provide a valuable resource for all those interested in birds of the region, particularly for those doing research. The Duck Mountain area is given special note, as it is sufficiently different from the rest of the area. For example, the Evening Grosbeak is variable in the parkland, but is resident at Duck Mountain.

The book contains several maps. The first is an excellent fold-out map of the area covered. It does not show roads (so it is uncluttered), but does depict towns, etc. There are several banding recovery maps. These are not labeled, but it is an obvious guess as to what they represent. They are identified obliquely in the acknowledgments as waterfowl migratory pathways by Kathy Meeres and locations where young were banded by Kelvin Wylie.

After reading this book I commented to a friend that the data given show the disappearance of the Passenger Pigeon was followed by the subsequent expansion of the Mourning Dove into this area. It was an interesting correlation. However, I had some difficulty in finding the pages to show him because there is no index. You must know the sequence of the current AOU 49th supplement to be able to find a species account.

The book has several useful appendices. The first gives a list of all the species seen in the area. This is followed by a summary of the Breeding Bird Surveys, then a list of banded species. Finally there is a list of waterfowl banders and their banding records.

I think these regional accounts are very important contributions to the record of knowledge. While this book may have limited sales in the local area and among a group of specialists, I believe it will be an important document for many years to come. In comparison to other similar works this is a scholarly and very professional product. The authors and the Saskatchewan Natural History Society are to be commended for undertaking this project.

ROY JOHN

2193 Emard Crescent, Ottawa, Ontario K1J 6K5 Canada

BOTANY

Northeastern Fern Identifier

By Richard S. Mitchell and Laurie Danaher. 1998. New York State Museum, Albany, New York. U.S. $19.95.

This computerized guide to 70 fern species of northeastern North America has been loosely based upon Eugene Ogden's *Field Guide to Northeastern Ferns*, published by the New York State Museum in 1981, one of the earliest publications to employ random-access keys in fern identification.

According to the introduction to the CD, "this package provides a menu-driven, fully color-illustrated guide and random-access key to ferns of the northeastern United States and eastern Canada. With it, the user may identify a fern by merely matching its characteristics with illustrations on screens provided. This allows a beginner to proceed with the identification of a fern after learning about five simple terms indicated on the help screen. As each feature of the fern in question is chosen, a decreasing number is displayed on the main screen, indicating how many regional fern species share that combination of characters."

Unfortunately, the Northeastern Fern Identifier is a DOS-based program. Its approach to interacting with a computer's video card is not compatible with recent operating systems, and it will not function on most computers running Windows NT, 2000, or XP. It will function on older computers running Windows 95 or 98. This is a serious limitation that means the program cannot be used on the vast majority of current computers. I was unable to contact the author by e-mail to determine whether or not a version more compatible with more up to date operating systems is planned.

Once a sufficiently out-of-date computer was found using Windows 98, an analysis of the efficacy of the program on the CD was carried out. Generally, it was found that the random access method can be as efficient as the traditional dichotomous keying method of species identification. The program allows the selection of any one of 24 identification options, including position of sori, indusia, vein branching, leafy margins, vascular bundles, etc. It then becomes possible to eliminate possible choices of species after each option selection, resulting in a decreasing number of applicable species. However, many of the selections result in a rather high number of possibilities making the selection process somewhat difficult. For instance, the two position of sori choices (marginal or not marginal) brings up 30 possibilities for marginal and 42 for non-marginal sori positions.

The photographs of the various species, mostly taken from 35 mm slides, are generally good, both in colour and clarity. Each page includes the name and possible synonyms of the species, the distribution range, habitat and description of similar species. It also includes, where applicable, a small photograph of the sori positions.

In general, the concept of a CD presentation of species identification methods has good potential. However, the *Northeastern Fern Identifier* requires an updated version if it is to be accepted and widely used by amateur botanists.

WILLIAM ARTHURS

1228 Lampman Crescent, Ottawa, Ontario K2C 1P8 Canada

Flora of the Hudson Bay Lowland and its Postglacial Origins

By John L. Riley. 2003. National Research Council of Canada, Research Press, Ottawa, Ontario, Canada. $49.95 (postage included).

The Hudson Bay Lowland is an area south and west of Hudson and James Bays measuring 325 000 square kilometers in northern Ontario, northeastern Manitoba and a small part of northwestern Quebec. In the introduction it is described as one of the Earth's largest more or less continuous wetland landscapes. The author describes its geology and glacial history, vegetation, soils, permafrost, and tree line, climate, climate change and other recent stresses and his objectives.

This flora is not like other floras such as *Vascular Plants of Continental Northwest Territories, Canada* by Porsild and Cody (1980) or *Flora of the Yukon Territory* by Cody (1996) which are organized in taxonomic sequence with keys, descriptions, habitat and range information in considerable detail. This book, however, does contain a wealth of information. In the Introduction section there is "Geology and glacial history information", "Descriptions of the vegetation, soils, permafrost and the tree line", "Climate, climate change, and other recent stresses" and "Objectives". This is followed by "Methods" which include a wealth of information under the titles "Data assembly and field surveys", "Data collection areas" and "Floristic analysis". Then Results information is provided under "Data collection areas", "Coincident distribution patterns" and "Floristic zonation". The next section entitled "Postglacial origins of the Flora" contains fine information and maps regarding "Early vegetation development", "Species migration", "Widespread species of the Hudson Bay Lowland", "Eastern species of the Hudson Bay Lowland", "Western species of the Hudson Bay Lowland", "Coastal species of the Hudson Bay Lowland", "Arctic species of the Hudson Bay Lowland", "Other themes in the flora of the Hudson Bay Lowland – including introduced and rare species". This is followed by Acknowledgments and References plus four pages which contain beautiful colour pictures of 32 species accompanied by four pages with pertinent information. All of the

above is to be found on the first 100 pages of the book.

The above is followed by Appendix A which is comprised of 148 most interesting distribution maps in alphabetical order by scientific name which, with combined dot maps with range-limit maps, provide precise distributional data from the Hudson Bay Lowland and related areas, while still indicating the broader distribution of the species. Appendix B entitled "Catalogue of the Vascular Plants of the Hudson Bay Lowland" is a summary of individual data collection areas in the Hudson Bay Lowland. This catalogue follows the order of families in Dalla Torre (1958) and Verdoorn (1938), with the taxa organized alphabetically within families. Appendix C, Excluded Records, has an alphabetical list of scientific names that have been excluded because of redetermination or because relevant voucher material could not be found.

The author is to be congratulated for putting together this most informative study of the terrain, plants and historic literature related to this extremely interesting area.

WILLIAM J. CODY

Biodiversity, Program on Environmental Health, Agriculture and Agri-Food Canada, Wm. Saunders Building, Central Experimental Farm, Ottawa, Ontario K1A 0C6 Canada

The War on Weeds in the Prairie West: An Environmental History

By Clinton L. Evans. 2002. University of Calgary Press. xvii + 309 pages. Paper $29.95.

During recent history, weed eradication has been a constant battle, with the balance usually tipped against the farmer. Evans documents this battle in the Canadian prairies between 1800 and the 1950s. His objective is to "highlight the shortcomings of the current noxious-weed legislation and crop production systems on the Prairies." He argues that the main result of legislation and its accompanying agricultural bureaucracy was to perpetuate an "ecologically unsound, weed-friendly style of farming." By identifying weeds as an "enemy", attention was diverted from the "true enemy", which Evans sees as "the extensive system of grain farming" entrenched in the agricultural system, encouraged by "a style of agriculture that actively cultivates weeds". Evans contends that hitherto little attention has been paid to weeds in the history of the Canadian west. Yet he believes that "weeds are important", not least because of the immense costs of weed control, the huge losses caused by weed infestations, and the enormous human effort directed to weed eradication. Evans comments that historians have exhaustively analyzed social and political activities of prairie farmers, while paying little attention to utilitarian issues, "mundane, practical activities" like weed control, that dominated their daily lives.

Evans demonstrates that weed definitions are not biologically based but are founded on utilitarian concepts. Crops are "useful" plants. Hence, any plant that competes with the crop is a "non-useful" plant or weed. Many weed plants are doubly "out of place" in western Canada because they are exotic. The main "villains" include Russian thistle (*Salsola pestifer*), tumble mustard (*Sisymbrium altissimum*), pennycress (*Thlapsi arvense*), and Canada thistle (*Cirsium arvensis*). Evans lists the biological attributes that contribute to "weediness" and make a plant a successful weed. These include good seed dispersal characteristics, an ability to spread vegetatively, morphological plasticity, profuse seed production, annual habit, broad ecological tolerance and, sometimes, perhaps phytotoxicity. He points out that farming activities have exerted evolutionary pressures on weeds, often enhancing their "weedy" characteristics. Weeds are, therefore, "cultural artifacts" just like the social and agricultural systems within which they flourish.

Next, Evans sets the historical context by examining farming practices and weed management in the UK, beginning in 1500, when most major components of the weed flora were already established in Britain. Subsequent generations of farmers developed and modified strategies, often labour-intensive, to deal with them, including late sowing, planting clean seed, crop rotation, manual weeding, hoeing and ploughing, and livestock pasturing. Summer fallowing and tillage, later widely applied in Canada, developed from medieval farming. Immigrant farmers brought this weed knowledge and control experience to North America. The weed battalions that British farmers battled are similar to those that plagued Canadian agriculture. Indeed, many weed species also traveled as inadvertent immigrants to North America.

European-derived settled agricultural communities first developed in eastern Canada. Evans concentrates on the development of weed control strategies and policies between 1800 and 1867 in what is now Ontario, a region that mainly looked to Britain for its knowledge of agriculture. Weeds were a problem by the 1830s, with increasingly strident and vociferous fulminations against them in newspapers and commentaries. Ontario's weed flora was dominated by European plants, especially Canada thistle. Eastern North America before European settlement was mostly forested. Therefore, imported weeds, adapted to open disturbed landscapes, had a competitive advantage over native forbs when land was cleared. Evans points out that for many settlers the "war on trees" was more important than the "war on weeds" in the early years. Perhaps more significantly and subtly, European weeds, having co-evolved with European agriculture for centuries, were preadapted to take advantage of the ecological niches offered in cleared agricultural landscapes. Evans observes that early 19th cen-

tury agriculture in Upper Canada was dominated by wheat production, driven by economic demand in Europe and the settlers' need to produce a cash crop quickly. The mode of production involved one year of cropping followed by a year of summer fallow with limited tillage. In Evans' view, this was inherently more "weed-friendly" than the longer four-course rotation then prevalent in Britain.

The war on weeds took a legalistic turn with the passage of the Canada Thistle Act in 1865, the first focused, noxious weed legislation. It attempted to control one weed by compelling landowners and managers to clear and eradicate it. Evans notes that the Act's efficacy was limited because landowners had little time or energy to undertake eradication and municipalities were unwilling or unable to enforce its provisions. Weed clearance was also predicated on an assumption of cheap and plentiful labour, a situation that did not prevail in Ontario. Evans sees this legislation as a clear break with the previously dominant British tradition. Interestingly, he sees it as an exemplar of "an emerging national identity."

Evans then shifts his attention westwards as agricultural settlement spread from Upper Canada to the prairies. Evans views this era (1867 – 1905) as a time of "paper diplomacy and intense propaganda" with "the entrenchment of a blindly oppositional view of weeds in response to the rapid advance of aggressive immigrant vegetation." New immigrant weeds, notably Russian thistle (*Salsola pestifer*), became important problems. When agriculture spread west, Evans records, the Ontario experience was repeated. The same pattern of "wheat mining" was established, with its concomitant spread of weeds, exacerbated by a government policy that saw prairie wheat production as essential for the national economy.

By 1906, Evans sees the war as fully engaged on the western front. He characterizes the next forty years (1906-1945) as an interval of increased bureaucratization in the battle against weeds, with a gradual shift from the goal of "eradication" to the more realistic one of "control". Evans draws parallels between the growth of military bureaucracy leading up to WWII and the expansion of agricultural bureaucracy with enhanced powers conferred through increasingly draconian legislation. These powers included seizure of infested land if landowners did not battle weeds sufficiently diligently. Weed inspections, enforcement campaigns, and educational programs formed part of the onslaught.

The transition to herbicides and chemical control began with postwar optimism when it looked as if science and technology could solve every problem. At first, 2,4-D, which became available in 1945, looked like the answer to the prairie weed problem. It was cheap, effective, and apparently safe. Farmers took to chemical control enthusiastically. However, Evans argues that herbicides merely postponed the inevitable consequences of "weed-friendly" agriculture by permitting prairie farmers to continue growing a limited range of predominantly grain crops, especially wheat, with short rotations and summer fallow. By the 1960s, widespread chemical use in agriculture had clearly produced new problems. Evans notes that chemical herbicides, while they did reduce broad-leafed weeds, exacerbated problems with grass-like weeds, such as wild oats. Evans also describes how by the 1970s, herbicide-resistant strains of some weeds were being reported, suggesting that weeds were modifying to cope with the chemical threat. With the recognition that chemicals were not the total answer came a change in language and rhetoric, with "weed management" becoming the objective by the 1980s, rather than "weed control".

Evans' discussion concentrates on the concept of "good husbandry", the totality of farming practice rather than maximization of crop production. Though he does not put it in these terms, this idea has much in common with the currently fashionable idea of "sustainability". Evans sees the "good husbandry" approach as perhaps the best solution to the weed problem. Quite how this could be implemented, in this era of agribusiness, he does not make clear. Evans' survey concentrates on the literature and experiences of British and English-speaking farmers, agricultural experts, and commentators. Yet the prairies became home to farmers from many different regions – including Ukraine, eastern Europe, and Scandinavia. Many weeds were familiar to these people as ones they had battled in "the old country". Did their approaches differ in any significant way from those of farmers raised in the British or Ontario tradition? Throughout, Evans' analysis focuses on arable (crop) farming, especially grain production, rather than ranching. Evans does not discuss range management in any depth, a curious omission given its importance in the Canadian west.

This book is absorbing and clearly written. Evans' arguments are provocative and well presented. They should be of interest to anyone concerned with recent landscape change and environmental history in western Canada.

ALWYNNE B. BEAUDOIN

Provincial Museum of Alberta, 12845 102 Avenue, Edmonton, Alberta T5N 0M6 Canada

ENVIRONMENT

Cliff Ecology: Pattern and Process in Cliff Ecosystems

By Doug Larson, Uta Matthes, and Peter Kelly. Cambridge University Press, Cambridge, UK. 340 pages. $105.

Larson, Matthes and Kelly set themselves a formidable task in writing *Cliff Ecology*. Most similar books focusing on other habitats draw on an extensive literature, which is shaped by the authors' experience into a (hopefully) unified and illuminating whole. However, as Larson et al. are quick to point out, cliffs are one of our most ubiquitous and least studied landscape features. Compared to habitats on level ground, cliffs have received almost no scientific attention. In reviewing this almost non-existent literature, the authors have shown that while we do not know much about cliffs, what little we do know is so intriguing that we ought to be paying a lot more attention to these places.

The study of cliffs is limited as much by the preconceptions of the scientists involved as by the inherent difficulties in sampling this environment. Larson et al. cite cases where researchers concluded that cliffs do not represent biological communities, despite having documented the unique biota of the cliffs in question. Similarly, the authors identify problems in studies linking plant distribution to substrate chemistry. In these cases the investigators' expectations lead them to misinterpret their own empirical data. Larson et al. argue persuasively that we know so little about cliffs in large part because of how much we thought we knew – an important reminder to scientists in any discipline.

In the face of our self-inflicted ignorance or "cliff-blindness", *Cliff Ecology* presents a very thorough refutation of the most egregious misconceptions. These aren't extreme, inhospitable places – chapters on geology and the physical environment show how the structure of cliffs moderates moisture, temperature and sunlight. Cliffs aren't lifeless – nearly 100 pages are devoted to reviewing the flora and fauna documented on cliffs around the world. They provide refuge for species otherwise extirpated from a region by competition, predation, human development or changing climate. Cliffs are not homogenous – from microscopic communities growing in the matrix of the rock itself to old growth forests rooting in cracks and fissures along the face, cliffs provide a surprising variety of habitats.

The authors have not limited themselves to the pure ecology of cliffs. They also venture into anthropological and sociological territory. They present a survey of the appearance of cliffs in magazine advertisements over a two year period as evidence of the cultural importance of cliffs as icons. I'm not entirely convinced by these data, but they do establish cliffs as a full-time passion for the authors themselves! More compelling arguments are presented in the chapter devoted to the relationship between humans and cliffs, with discussion that ranges from prehistoric cave paintings, bonsai collecting, and seabird harvesting, to rock climbing, real-estate development and quarrying. Underlying this discussion is the authors' "urban cliff hypothesis", in which they propose that early human cultures developed in caves along cliff faces, and that modern cities and agricultural systems are the result of our exporting the biota and physical characteristics of cliffs to the broader landscape. It's an intriguing idea that will be further explored in an upcoming book from the same authors.

This is not intended to be the definitive work on cliffs. Rather, Larson et al. have prepared a strong case encouraging more concerted work examining cliffs as biologically meaningful places. That the treatment is uneven in places reflects real gaps in knowledge more than any deficiency on the part of the authors – many of the sources, particularly relating to flora and fauna, are not studies of cliffs *per se*, but are gleaned from more general work that included cliffs only incidentally. I expect the book as a whole will provide a major point of departure for future research on cliffs. Far more detail is presented than will be of interest to general audiences, but there are more than enough revelations about the nature of cliffs to reward the interested reader.

TYLER SMITH

155 Vanguard Avenue, Pointe Claire, Quebec H9R 3T4 Canada

Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest

Edited by Richard O. Bierregaard, Jr, Claude Gascon, Thomas E. Lovejoy, and Rita Mesquita. 2001. Yale University Press, New Haven, Connecticut. 478 pages. U.S. $65.

Beginning as a seemingly basic and simple study on the minimum size of a viable rainforest ecosystem, this over-20-years-and-counting project is the largest and most ambitious investigation into the effects and consequences of habitat fragmentation in the tropics. The key visionaries present an edited volume with some technical contributions by researchers actively building upon our knowledge of the Amazon but also with a primary intent on getting the broader message of management and conservation of a very complex environment to a wider audience including wildlife managers and government policy makers. After two decades of research, some by trial and error as the practical concept changed from the smallest area to differing fragment sizes, this is a timely summary of progress and conclusions that can now hopefully be translated into effective application throughout the world.

The book is divided into five sections covering an overview of the project and underlying philosophy, general forest ecology of Amazonia, effects of fragmentation on different organisms, guidelines and issues for management, and ending with a synthesis aimed at conservation in Brazil. Part 1 has four chapters starting with an historical perspective on the genesis of what is now known as the Biological Dynamics of Forest Fragments Project. The theoretical underpinnings are based largely on the influential island biogeography developed by MacArthur and Wilson but fragmented habitats require a reinterpretation of ecological processes to account for observed species richness. The book is definitely aimed at the unnatural phenomenon of human induced deforestation and understanding the unique effects produced by forest edge and surrounding modified habitat. The first part finishes with a description of the study site 80 km north of Manaus, methodology of isolating the experimental forest fragments, and brief overview of data accumulated to date.

Part II looks at the ecology of the Amazonian forest concentrating primarily on the tree community. An in-depth study was conducted on the Brazil nut tree family (Lecythidaceae) in a 1000 hectare control site within continuous forest and will serve as baseline data for comparative purposes with fragmented habitats. Carbon dating was done for aging trees because in the tropics annual growth rings are not reliable. This facilitated extrapolation to areas of population dynamics, genetic diversity, and carbon cycling. The last chapter in the section investigates the significance of rarity in trees, their genetic basis, and the ecological and evolutionary implications for tropical forests.

The bulk of the book deals with the effects of fragmentation on plant and animal communities. Some of the studies on plants include the edge effect on population structure and dynamics as related to tree mortality and recruitment; case study using palms to investigate demography and community composition; seedling ecology and forest regeneration; and habitat change on the pollination of the large timber tree *Dinizia excelsa* by bees. There are invertebrate studies of fragmentation effects on fruit flies and changes in their guild structure; metapopulation dynamics of the social spider *Anelosimus eximius*; response of ants in the modified matrix habitat surrounding the forest fragments; species composition of stingless and orchid bees with comparisons to other neotropical localities; and the effects on vertebrate predators of changes in leaf-litter invertebrates. The impacts of forest fragmentation on vertebrate communities are investigated by studies on frog community structure and breeding success; diversity and abundance of understory birds in modified matrix habitat; summary of primate projects conducted in the study area; and a detailed look at home range and diet of the brown capuchin monkey (*Cebus apella*).

The fourth section deals with management related issues pertaining to the Amazon. The first chapter takes a close look at soil quality in the research site and the general inappropriateness of Amazonia for large-scale agricultural or ranching purposes. Pastures are, however, shown to be restorable to regrowth vegetation with potential for reforestation. The role of fire is also explored in the regeneration of rainforest. Selective logging is seen as economically viable if treated as a primary industry as opposed to a by-product of clear cutting for ranching or farming. Different edge effect models were used to test their application across a variety of landscapes for comparative purposes throughout the tropics. Remote sensing facilitates landscape perspectives of fragmented patches, surrounding matrix habitat and continuous forest, and interpretation of change by spatial analysis to characterize and monitor the observed patterns.

The last part and chapter is a synthesis of 20 years of study in a fragmented forest research area and the lessons learnt in the form of principles that can be applied to wisely balance the needs of conservation and sustainable development in the Amazon and beyond. Whether these principles will be adopted and implemented over the long term depends on the will of the government of the day but this book and the research contained within each chapter has laid the groundwork for sound policy decisions. *Lessons from Amazonia* is a must read for tropical biologists, environmental managers, and government policy makers. I hope to see another volume in two-decades time giving an update on the future progress.

BURTON K. LIM

Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6 Canada

MISCELLANEOUS

The North Runner

By R. D. Lawrence. 2003. Natural Heritage Books, P.O. Box 95, Station O, Toronto, Ontario M4A 2M8 Canada. 288 pages. $22.95 Cloth.

The North Runner, R. D. Lawrence's eleventh book, was first published in 1979 and re-issued in 2003, and it covers events in his life in the mid 1950s. A "North Runner" is a northern sled dog that made possible the harvesting of furs as well as carrying people and supplies across Canada's northern lands. As well these northern sled dogs contributed to successful expeditions to both the North and South Poles.

The North Runner of this book – Yukon by name – was part wolf and part malemute. Malemutes were bred to pull heavy loads all day in incredibly cold weather. Although stubborn and independent, with early training they could become wonderful companions to their owner.

Lawrence, born in 1921 of an English father – a journalist – and a Spanish mother, spent his somewhat lonely childhood in Spain. In his early teens he fought with the antifascists against Franco, then escaped to England. There he enlisted in World War 2 and fought in Europe and North Africa. The senselessness of war hardened him towards death and caused him to withdraw from personal relationships and friendships.

After the war, with his love of nature, he studied biology at Cambridge University for a few years but became impatient with the method of teaching. Tired of people and cities, he emigrated to Canada in the mid-1950s where he worked at a variety of jobs in Toronto and saved enough to purchase a homestead of a 100 acres near Fort Francis in northwestern Ontario. He obtained a timber contract locally which he proposed to fill from the woods on his land. Needing dogs to pull a sled loaded with timber, he obtained three huskies but needed a strong leader. A local Indian brought him a half-starved, dirty, angry dog which the Indian controlled with a club. Strangely, Lawrence found himself drawn to this snarling creature. He purchased it and using food and soft words gradually won this fierce, angry dog's trust. Eventually the joy and affection which each showed the other broke down Lawrence's antipathy to the world.

Together they would journey across Canada in a 'battered Chevrolet' and with Yukon's curiosity about everything, Lawrence found himself increasingly aware of the details of his surroundings. He describes with great sensitivity, the beauty of the natural world around him. One is made to feel part of this world as he tells of bird songs, rushing water, blinding blizzards, sunlit meadows, leaping hares and even a tornado, all in vivid, beautiful prose.

Out hunting for meat one day with Yukon, he found himself in the path of a moose which was acting in a demented manner. The dog attacked and brought down this crazed animal which Lawrence was forced to shoot. Guessing the meat unfit to eat, Lawrence took tissue samples to seek out possible cause for the animal's behaviour. Later he examined the tissues under his microscope and discovered worms in the brain tissues which he thought probably caused the moose's unnatural behaviour.

There is a vivid description of Yukon chasing a marauding bear through the woods. Despite Lawrence's search, the dog seemed to have gone. Three days later a bloodied, torn dog banged on the window much to Lawrence's joy and relief. He realized what a friend and companion this dog had become.

After traveling to northern British Columbia to discover the source of the River Nass and spending a winter up there in isolation, he decided to drive with Yukon, to Winnipeg where he found a job as a journalist. There he met and fell in love with a librarian named Jean. Faced with a dilemma of married life and work in the city versus life in the wild with Yukon, he returned to try and sort things out at his old homestead where Yukon solved the problem in his own way.

A further source of information about Lawrence can be found in his 1994 memoir *The Green Hills Beyond* which explains fully in his own words when and why he decided to become a "nature watcher". Sadly he died in October 2003.

ROBINA BENNETT

38 Parkland Crescent, Nepean, Ontario K2H 7W5 Canada

Seasons of the Arctic

By Paul Nicklen and Hugh Brody. 2000. Greystone Books, Vancouver, British Columbia [in the United States: Sierra Club Books (Random House Inc.)]. 102 pages. U.S. $32.

There is no shortage of books about the Arctic, nor of photographs, but this collection of photographs is exceptional. Paul Nicklen has lived in several areas of the Arctic since 1971, and his love for the wildlife and scenery is apparent in every shot. How has he managed to find animals in such unique situations as the heads of two tiny polar bear cubs peering at the camera over the back of their mother, so close you can see only part of her back? Or three sandpipers neatly surrounded by discarded caribou antlers, reflecting in still water? The book cover shows the head of a wet polar bear, shaking like a dog, with every drop of water silhouetted against the sky.

Nicklen has ranged the Arctic for years, sometimes alone for three months at a time, capturing extraordi-

nary and unconventional images such as a time-lapse shot of stars moving around the fixed North Star. Hugh Brody, who wrote the short introduction, is a poet, and his prose shows it. He speaks of Nicklen's "immaculate portraits of the natural world". There are no human beings in any photographs, but they are represented by the title "Seasons", which does not refer to our usual four, but the six seasons northern people use to divide the year – an early spring and early autumn season with their own names added. We may think the Arctic is a bare, barren place, but these portraits illustrate the teeming life above and below the snow, land and water which sustains a flourishing ecosystem. It is a beautiful book.

JANE ATKINSON

255 Malcolm Circle, Dorval, Quebec H9S 1T6 Canada

When the Wild Comes Leaping Up: Personal Encounters with Nature

Edited by David Suzuki. 2003. Greystone Books, Vancouver, British Columbia. 235 pages. $22.95.

This latest anthology of nature writings, edited by Canada's pre-eminent scientist and writer David Suzuki, brings together new essays by a breadth of writers. Some of the authors were familiar to me as nature essayists (Diane Ackerman, Rick Bass, Sharon Butala, Wade Davis, Bill McKibben, David Quammen, David Suzuki); others were familiar authors, though not as nature writers (Margaret Atwood, Timothy Findley); while the rest were entirely new (Robert Drewe, Richard Flanagan, Jennifer Potter, Beth Powning, David Reynolds, David Adams Richards). Geographically, they hail from Canada, the USA, Great Britain and Australia.

Suzuki asked the writers to "share an experience that moved them or changed them in some way and that occurred in the natural world" because he argues that preservation of the wild is ultimately about people connecting with nature in a spiritual way, rather than relying on intellectual arguments for biological diversity or economic value.

Many of the stories are woven around moments or events in the authors' lives that influenced them tremendously. Rick Bass contemplates when, how and why these moments occur: "Who knows what moments – what complications of the physical and the mental – of landscape and story – conspire to ignite the sparks of enduring memory, formative or pivotal or living memories?" And do these moments only occur in pristine wilderness or can they occur in the humanised environment? The essays by the British authors, set in a small park, a country lane and a commons – tamer versions of the natural world than the Montana where Bass lives – suggest that nature's power can be felt in both. Diane Ackerman agrees, writing about how backyard animals such as deer, squirrels and birds become the entryway to the bustling world of nature for many suburbanites and travellers.

All of the authors write with passion and eloquence, and because of the personal nature of the essays, most readers will find themselves connecting with the stories. This book is an enjoyable antidote to the important, though often depressing, ones detailing destruction of the natural world.

CYNDI M. SMITH

Box 5, Waterton Park, Alberta T0K 2M0 Canada

NEW TITLES

Zoology

***Birds of Chile**. 2003. By A. Jaramillo. Princeton University Press, Princeton, New Jersey. 240 pages. U.S. $29.95 paper, U.S. $55. cloth.

***Birds of Manitoba**. 2003. Edited by Peter Taylor et al. Manitoba Naturalists Society, Winnipeg, Manitoba. viii + 503 pages.

***Freshwater Fishes of Manitoba**. By K. Stewart and D. Watkinson. 2004. University of Manitoba Press, St. John's College, University of Manitoba, Winnipeg, Manitoba, R3T 2M5 Canada. 360 pages. $29.95 paper, $44.95 cloth.

Hawks and Owls of the Great Lakes Region & Eastern North America. 2004. By C. Earley. Firefly Books Ltd., 3680 Victoria Park Avenue, Toronto, Ontario, M2H 3K1 Canada. 128 pages. $16.95 paper, $24.95 cloth.

***Owls of the World**. 2003. By J. Duncan. Key Porter Books, Toronto, Ontario. 319 pages. $60 cloth.

***Raptors of Eastern North America**. 2003. By Brian Wheeler. Princeton University Press, Princeton, New Jersey. 456 pages. U.S. $45 cloth.

***Raptors of Western North America**. 2003. By Brian Wheeler. Princeton University Press, Princeton, New Jersey. 580 pages. U.S. $49.50

***Wild Mammals of North America, Biology, Management and Conservation (2nd Edition)**. 2003. Edited by G. Feldhamer, B. Thompson, and J. Chapman. Johns Hopkins University Press, 2715 N. Charles Street, Baltimore, Maryland. xiii + 1216 pages. U.S. $175 cloth.

Botany

***Alpine Plants of North America: An Encyclopedia of Mountain Flowers from the Rockies to Alaska**. 2003. Edited by Graham Nicholls and Rick Lupp. Timber Press. 344 pages. $49.95 cloth.

† **Cape Cod Wildflowers**. 2003. By M. Di Gregorio and J. Walner. University Press of New England, 37 Lafayette Street, Lebanon, New Hampshire. 184 pages. U.S. $19.95 paper.

Sea Legs: Tales of a Woman Oceanographer. 2003. By K. Crane. Westview Press, Boulder, Colorado. 320 pages.

A Magic Web: The Tropical Forest of Barro Colorado Island. 2003. By E. Leigh. Oxford Press, New York, New York. 292 pages. U.S. $40.

* **The Wild Orchids of North America/North of Mexico.** 2003. By P. Martin. University Press of Florida, 15 Northwest 15th Street, Gainesville, Florida. U.S. $27.95 paper, U.S. $45.95 cloth.

Environment

†**Conservancy: The Land Trust Movement in America**. By Richard Brewer. 2003. University Press of New England. 320 pages. 6 × 9". U.S. $29.95 cloth.

Children's Books

Aliens from Earth: When Animals and Plants Invade Other Ecosystems. 2002. By M. Batten. 2003. Peachtree Press, Atlanta, Georgia. 48 pages. U.S. $15.95

Black Bear: North America's Bear. 2003. By S. Swinburne. Boyds Mills Press Holmesdale, Pennsylvania. 32 pages. U.S. $15.95

Born to be Wild – Bears: North America. 2003. By K. and K. Ward. Wildlight Press Inc., Santa Cruz, California. 24 pages.

Ducks. 2003. By M. Mitchell. Lerner Press, Minneapolis, Minnesota. 24 pages. $15.93.

Frogs Sing Songs. 2003. By T. Oliver Charles Bridge Press, Waterton, Massachusetts. 32 pages. U.S. $16.95

Honey Bees. By M. Rustad; **Cockroaches**. By M. Rustad; Butterflies. By M. Schub; and **Termites.** By M. Schub. 2003. Consulting Editor G. Saunders-Smith. Pebble books, Minneapolis, Minnesota. Each 24 pages and U.S. $14.60

Wolves. 2003. By A. Royston. Amart Apple Media, North Mankato, Minnesota. 24 pages. U.S. $21.35.

Miscellaneous

Mastering Digital Photography and Imaging. 2004. By P. Burian. Firefly Books, 3680 Victoria Park Avenue, Willowdale, Ontario M2H 3K1 Canada. 304 pages, paper $41.95.

† Available for review
* Assigned for review

News and Comment

Point Pelee Natural History News 3(3)

The fall 2003 issue, volume 3, number 3, pages 37-52, contains: Point Pelee Memories: 1956-1999 (William A. Martin) — Noteworthy Bird Records: June to August 2003 (Alan Wormington) — Point Pelee Butterfly Count: August 9, 2003 (Sarah E. Rupert) — Record-late Warblers at Point Pelee: Spring 2003 — In the Field [Lake Chubsucker: still present in Pelee Marsh; Bullfrog: still present in Pelee Marsh; More Black Witches at Point Pelee: Summer 2003; Eurasian Tree Sparrow: Second Record for Point Pelee; Record-late Carolina Wren nest for Point Pelee] — News and Announcements: W. E. Saunders Birding Odyssey: September 6, 2003; New Publication on Pelee Island; OFO Annual Meeting (2003) held at Leamington — Upcoming Events and Outings.

This newsletter for Point Pelee National Park, Ontario, is published by the Friends of Point Pelee and edited by Alan Wormington (e-mail:wormington@juno.com). Editorial Assistants are Gordon D. Harvey and Michelle T. Nicholson. The web site is www.wincom.net/~fopp/Natural_History_News.htm. Back issues of volumes 1 and 2 are available for $15 per volume/ $5 per single issue.

Froglog: Newsletter of the Declining Amphibian Populations Task Force (59,60)

Number 59, October 2003. Contents: DAPTF Seed Grants 2004 — It's Not Carnival for the Harlequin Mantella! Urgent Actions Needed to Conserve *Mantella cowani*, an Endangered Frog from the High Plateau of Madagascar (F. Andreone and J. E. Randrianirina) — Amphibian Biodiversity Recovery in a Large-scale Ecosystem Restoration (Bob Brodman) — Amphibian Mortality by Road-Kill in a National Park (John Serrao) — Amphibians in Argentinean Soybean Croplands: Implications for Biological Control (R. Lajmanovich, P. Peltzer, A. Attademo, & W. Cejas) — Reports on DAPTF Seed Grants — Froglog Shorts.

Number 60, December 2003. Contents: Populations of Two Species of Forest Frogs, Genus *Platymanis*, are Diminishing on Negros Island, the Philippines (C. N. Dolino, E. L. Alcala, and A. C. Alcala, DAPTF WG Chair, Philippines) — Action Plan for Sustainable Exploitation of *Rana ridibunda* stocks from the Danube Delta Biosphere Reserve (Romania) (Zsolt Torok) — Report of a Breeding Aggegation Extirpation of an Endemic Marsupial Frog, *Gastrotheca christiani*, in Argentina (Marcos Vaira) — Non-finding of the Kenyan Endemic Frog *Arthroleptides dutoiti* (Stefan Lotters, Damaris Rotich, and Michael Veith — Reports of DAPTF Seed Grants — DAPTF Rapid Response Fund — Book Offer for DAPTF Members — Froglog Shorts.

Froglog is the bi-monthly newsletter of the Declining Amphibian Populations Task Force of The World Conservation Union (IUCN)/Species Survival Commission (SSC) and is supported by The Open University, The World Congress of Herpetology, and Arizona State University. The newsletter is edited by John W. Wilkinson, Department of Biological Sciences, The Open University, Walton Hall, Milton Keynes, MK7 6AA, United Kingdom; e-mail: daptf@open.ac.uk. Funding for *Froglog* is underwritten by the Detroit Zoological Institute, P. O. Box 39, Royal Oak, Michigan 48068-0039, USA. Publication of issues 59 and 60 was also supported by Peace Frogs www.peacefrogs.com and by RANA and the US National Science Foundation grant DEB-0130273.

Amphibian Voice Summer 2003

Volume 13, number 2, contains — Citizens Saving Turtles: Turtle S.H.E.L.L. Tortue: Helping turtles across the road (Bill Bower) — Lily pads & cattails: Adopt-a-pond updates (Sara Ingwersen) — Kawartha turtle trauma centre: 2003 update (Kristy Hiltz) — Ribbet's Review (Alison Ronson) — Setting up turtle crossing signs in your community: A step by step guide from the members of the community environment network in Bancroft (Daniel Boileau) — Call'um of the wild: Rescuing turtles in war-torn Bosnia (Wes von Papineau) — Life as a 'turtler' at Algonquin Park's wildlife research station (Sara Boivin-Chabot, Jenny Kellar and Phung Tran) — A turtle-rific quiz.

Amphibian Voice is distributed to schools and communities participating in the Adopt-A-Pond programme. The newsletter's purpose is to provide information of amphibian, turtle, and wetland conservation issues and efforts in Ontario. It is edited by Sara Ingwersen and Bob Johnson. Adopt-A-Pond is a non-profit wetland education program supported by grants and private donations. Cheques for the latter should be made payable to "Toronto Zoo" and sent to Adopt-A-Pond, Toronto Zoo, 361A Old Finch Avenue, Scarborough, Ontario M1B 5K7; Fax (416) 392-4979; aap@torontozoo.ca.

Marine Turtle Newsletter (102)

October 2003. 32 pages: EDITORIAL: Changes at the MTN — ARTICLES: satellite tracking of the post-nesting migration of a Green Turtle (*Chelonia mydas*) from Hong Kong — First report of an association between *Planes cyaneus* (Decapoda: Grapsidae) and the Loggerhead Sea Turtles in the southwestern Atlantic Ocean — Hawksbill Turtles in seagrass beds — Loggerhead nesting effort and conservation initiatives at monitored beaches of Greece during 2002 — NOTES: Loggerhead Sea Turtle tagged in Brazil caught by a trawler in waters of the common Argentinian-Uruguayan fishing area — MEETING REPORTS — BOOK REVIEWS — ANNOUNCEMENTS — NEWS & LEGAL BRIEFS — RECENT PUBLICATIONS.

The Marine Turtle Newsletter is edited by Brendan J. Godley and Annette C. Broderick, Marine Turtle Research Group, School of Biological Sciences, University of Exeter, Exeter EX4 4PS United Kingdom; e-mail MTN@seaturtle.org; Fax +44 1392 263700. Subscriptions and donations towards the production of both the MTN and its Spanish edition NTM [Noticiero de Tortugas Marinas] should be made online at www.seaturtle.org/ntm or c/o SEATURTLE.ORG, 11400 Classical Lane, Silver Spring, Maryland 20901 USA.

Recovery Strategy for Bowhead Whales in Canadian Eastern Arctic

In 1980 the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) listed the population of Bowhead Whales (*Balaena mysticetus*) in the Canadian Eastern Arctic as Endangered. For the past several years, the Department of Fisheries & Oceans has worked in collaboration with the Nunavut Wildlife Management Board and the World Wildlife Fund to develop a Conservation Strategy aimed at promoting the recovery of this population of whales. The Strategy is now posted in English, French and Inuktitut on Environment Canada's Species At Risk web site and a PDF file version can be ordered from there: www.speciesatrisk.gc.ca/publications/plans/default_c.cfm

Bound hardcopy and CD versions of the Conservation Strategy will be available. Paper copies will be printed in English/Inuktitut and English/French; the CD will contain English, French, and Inuktitut versions. Can be ordered by mail from Holly Cleator, Marine Mammal Species At Risk Biologist, Arctic Research Division, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba R3T 2N6 Canada; or e-mail fwisar@dfompo.gc.ca.

National Recovery Strategy for Species at Risk in the Sydenham River: An Ecosystem Approach

This is National Recovery Plan Number 25, dated 23 October 2003, 72 pages. It was prepared by A. J. Dextrase, S. K. Staton, and J. L. Metcalfe-Smith on behalf of the Sydenham River Ecosystem Recovery Team. The two main branches of the Sydenham River drain into Lake St. Clair through the Carolinian Zone in southwestern Ontario. They support at least 34 species of mussels and 80 species of fish. Five of the mussels, eight of the fishes and one turtle have been listed nationally by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Summaries are given for all 14 of these species, some of which are found nowhere else in Canada. The Sydenham watershed is of judged to be of global significance to their conservation. Other sections discuss recovery goal, short-term objectives, overall strategies/approaches to recovery (management, stewardship, research, monitoring, community awareness and outreach, recovery and survival habitat, actions already completed or under way, knowledge gaps, links to existing management plans, recovery action groups and plans, potential impacts of recovery strategy on other species/ecological processes, and evaluation.

Additional information can be obtained by contacting the Recovery Team Chair, was Alan Dextrase, Ontario Ministry of Natural Resources, 300 Water Street, Peterborough, Ontario K9J 0M5 Canada. Copies of this report are available from Recovery Secretariat c/o Canadian Wildlife Service, Environment Canada, Ottawa, Ontario K1A 0H3 Canada. E-mail RENEW@ec.gc.ca. See also Recovery web site: www.speciesatrisk.gc.ca/recovery/default_e.cfm.

Recovery: An Endangered Species Newsletter (25)

The October 2003 issue contains: RECOVERY HIGHLIGHTS: SARA [Species At Risk Act] Proclaimed [5 June 2003] — Marmots released [two pairs of captive-raised Vancouver Island Marmots, *Marmota vancouverensis*, released near Nanaimo] — Record season for Whooping Cranes [*Grus americana*: 61 breeding pairs at Wood Buffalo National Park in 2003] — SPECIAL REPORT: The Species at Risk Act — How it works [Simon Nadeau]; Prohibitions under SARA — NEWS BITES: Reintroducing [Leopard] frogs [*Rana pipiens*] in Alberta [Kris Kendell] — Introducing [Leopard] frogs in B. C. — HSP [Habitat Stewardship Program] update — ESRF [Endangered Species Recovery Fund] update — COSEWIC [Committee on the Status of Endangered Wildlife in Canada] — FIELD NOTES: Two recovery approaches for the Roseate Tern [*Sterna dougallii*] [Andrew Boyne] — New [species considered at risk] list created in Quebec [Pierre Laporte] — ANNOUNCEMENTS: Awards — Upcoming events — Site Seeing — FEATURED SPECIES: Tracking the Eastern Wolf [*Canis lupus lycaon*] [Melanie Bernier].

Published by the Canadian Wildlife Service of Environment Canada, Ottawa, Ontario K1A 0H3. Edited and designed by West Hawk Associates. Recovery online: www.speciesatrisk.gc.ca/publications/newsletter/oct03/default_e.cfm

"This is the final issue of *Recovery*. The Canadian Wildlife Service will continue to offer information on recovery activities in other formats."

The Ottawa Field-Naturalists' Club Awards for 2002

IRWIN M. BRODO, CHRISTINE HANRAHAN, BEVERLY MCBRIDE, and SHEILA THOMSON

At the Club's Annual Soirée, held 26 April 2003, at St. Basil's Church in Ottawa, awards were once again given to members, and one non-member, who distinguished themselves by accomplishments in the field of natural history and conservation, or by extraordinary activity within the Club. As is frequently the case, there were no winners for a few of the OFNC awards this year. The following citations for those who did receive an award, however, were read to the members and guests assembled for the event.

Bill Royds – Ottawa Field-Naturalists' Club Member of the Year – 2002

The Ottawa Field-Naturalists' Club has a long history of active, committed members. Many of its committees have benefited greatly from the participation of volunteers with a particular expertise. The OFNC Conservation Committee, which has been actively working to preserve our natural heritage for more than three decades, continues to attract knowledgeable and committed members such as Bill Royds.

The Conservation Committee is one of the more high-profile committees in the club with its members attending meetings, open houses and most importantly, representing the club on any number of other committees outside of the OFNC. It reflects well on the club when these folks are able to contribute substantially to the work being carried out. One of Bill's biggest contributions, and one of his strengths, is his solid understanding of federal, provincial and municipal legislation. Bill not only has such knowledge at his fingertips, but he keeps abreast of changes and developments, which makes him absolutely invaluable since he can answer any question about almost any piece of legislation and give advice on how it works. Bill is especially knowledgeable about proposed and current municipal legislation for the City of Ottawa, which made him a natural to lead in the preparation of the OFNC Brief for Drafts 1 and 2 of the new Ottawa Official Plan. During 2002 he spent a huge amount of time making sure that the OFNC's views on natural areas preservation were clearly and cogently represented.

Bill is a very enthusiastic naturalist, as anyone who has attended a nature walk with him will attest. It is no doubt this deep appreciation for nature that drives his total commitment to protecting natural areas and the environment. He works exceptionally hard to make a difference wherever and whenever he can and is so involved in so many volunteer activities (in addition to working full time) that many of us wonder whether he has found a magic solution for stretching the 24-hour day. But no …his wife says he gets by on just four hours sleep per night!

Bill's contributions to the OFNC extend well back before 2002, but during this last year he has been particularly active in serving as the link between the OFNC and the Greenspace Alliance of Canada's Capital (GACC). He joined the Greenspace Alliance shortly after it was formed in October 1997 and quickly became an integral part of that dynamic group, serving as its Vice-chair and currently, as its Co-chair. As webmaster for the GACC's website, Bill is able to ensure an efficient exchange of information, which means that the OFNC and the GACC can cooperate profitably on ideas and issues, as the need arises, to the benefit of both groups.

One exceptionally high-profile project that Bill initiated, and worked hard to gain recognition for, is the "Poet's Pathway." This celebration of Canadian Poets and the landscape they loved will almost certainly be an enduring contribution to the Nation's Capital. Conceived of as a 30 km U-shaped route from Beechwood Cemetery to Britannia Bay with the Southern Corridor as a focal point, this is now being discussed with the National Capital Commission and the literary community.

Bill's contributions on behalf of the Ottawa Field-Naturalists' Club and the community have been particularly outstanding this year, and he is a fitting recipient of the 2002 Member of the Year Award.

David Hobden – George McGee Service Award for 2002

This year the Ottawa Field-Naturalists' Club recognizes the contributions of David Hobden with the George McGee Service Award.

For over five years, David has been a very active member of the club's Conservation Committee and the Fletcher Wildlife Garden Committee, dealing with all committee affairs with quiet competence, but always with a glint of humour in his eyes.

Since joining the Fletcher team in 1998 David has served the committee in many ways. Five years ago, David stepped in as Treasurer producing the regular, reliable financial statements committee members rely on to plan their many projects. A few years later, David became chairperson, first in an acting capacity, later assuming full responsibility. Four years ago he took over as Fletcher's liaison with landowner Agriculture Canada. He is currently leading critical negotiations with the Department on the use of the property and building that are at the very foundation of Fletcher Wildlife Garden. He has amassed a team of volunteers with expertise in various aspects of business and contracts to assist him. To quote a committee member, "His patience and perseverance have made our relationship with the Department one of mutual trust and respect."

David is a proven leader and organizer in such diverse tasks as hiring summer staff, developing the Fletcher's long-term plan and representing the Fletcher's interests on the Ottawa Field-Naturalists' Club Council. He continually demonstrates his ability to work together with others, to contribute wisdom and thoughtfulness, and to make well considered, effective decisions.

A lot of business acumen goes into keeping the Fletcher Garden humming along, but David has an artistic side too. Much of the garden's photo collection is David's work, all carefully labelled with name, date, and location.

David has been an OFNC member since the 1960s but he waited for the blessing of retirement to jump in as a volunteer. When he did, he also joined the Conservation Committee, where he is an active and devoted member, rarely (if ever!) missing a meeting. He attends public fora, prepares briefs and edits and comments on those written by others. One committee member noted, "When David offers a comment at a meeting, everyone listens, because we know it will be thoughtful and thought-provoking. Most importantly, he picks up on things that many of us forget or lose sight of in our haste to make a quick point."

A professional biologist, David received his PhD in England where he studied the bioaccumulation of trace elements in bivalves. He moved to Canada shortly after completing his studies. He was a biology professor at the University of Ottawa for most of the 60s. Then, until his retirement, he taught many levels and types of biology courses at Algonquin College. His students were fortunate to benefit from David's many fine qualities and dedication to his profession, just as his OFNC colleagues are now benefiting from these same qualities and dedicated volunteer service to the Club.

Philip Fry – Conservation Award for Members – 2002

Habitat destruction is a modern environmental problem that concerns many of us. Most people deal with it by joining environmental organizations like the Ottawa Field-Naturalists' Club and petition our governments to establish parks, spare woodlots and protect wetlands on the lands they manage. Philip Fry has taken a more direct approach. In 1984, he purchased six hectares of abandoned farmland near Oxford Mills and established a refuge for orphaned and threatened wild plants, calling it "The Old Field Garden." Philip was dismayed at the number of wildflowers, many of them rare, that succumb to the bulldozer, and so, although in his day job he was a professor of art history at the University of Ottawa and not a conservation biologist or horticulturist, he set about rescuing as many of these threatened plants as he could.

On his property, he studied the soils, water conditions and topography and meticulously drew up a plan of his land. He thinned cedar stands, dug ponds and added to the forest loam in order to develop as natural a community of native plants as he could, starting with thousands of plants rescued from land about to be destroyed by development. So successful was his approach that other wild plants of the region (not to mention scores of animals) took up residence at the Old Field Garden without any intervention. The successful rehabilitation of this unused farmland is a model for others, and people come from far and wide to see what he has done and how they can accomplish the same thing with their own property, or parts of it.

Philip's techniques for wildflower propagation and establishment developed by careful experimentation over the past 18 years are now shared with the general public through educational workshops and tours of the Garden, and the products of this propagation are now available for all who are interested in establishing wildflower gardens.

The Ottawa Field-Naturalists' Club recognizes Philip Fry's outstanding contribution to the conservation of native plants and re-establishment of wildlife habitat on abandoned lands in southern Ontario, by awarding him this year's Conservation Award for Members.

Michèle André-St. Cyr – Conservation Award for Non-Members – 2002

Many people by now have probably seen the "Turtle Crossing" signs at various locations in the Ottawa region, including at Britannia. These signs are the result of the work of one woman, Michèle André-St. Cyr of Rockland. Michèle's story is an inspiring one for it shows what one individual can do when motivated by a desire to bring about change.

While many people are concerned about protecting wildlife, few of us really translate that concern into action. Michèle André-St. Cyr is someone who did. Some years ago, concerned about the high number of turtles she was finding dead on the roads, she decided to do something about the problem. After much thought and discussion she produced a creative yet simple solution: Place "Turtle Crossing" signs at known turtle crossing sites along major roads. Much research and analysis went into their design and the result is a diamond-shaped yellow sign showing a black turtle with tire tracks on its back and black lettering in French and English indicating the months when turtles are most likely to be on the move: May-June.

In 2000, with design in hand, Michèle then got busy writing letters, contacting other knowledgeable people, and making presentations to the (then) City of Cumberland. The City, moved by her initiative and determination, agreed to the erection of these signs, provided she came up with the funding. Undaunted, Michèle set about seeking donations and along with money from her own pocket, had soon acquired the necessary funding to place the signs. That first year 14 signs were placed on local roads. Plans were soon underway to convince the new City of Ottawa to permit similar signs throughout the area and this is now being done.

As word of her work spreads, Michèle is now being contacted by interested individuals and communities from across the province, looking for advice on how they too might follow her lead. As of March 2003, numerous municipalities in Ontario have adopted her idea and her design, and interest has been expressed from outside Ontario.

Not content to rest once the signs had become a reality, Michèle formed the group TURTLE S.H.E.L.L./TORTUE S.H.E.L.L, of which she is current President. Their mandate is to educate and train "teachers, students, public officials and other members of the general public" about the life and ecology of Ontario turtles and instill respect for these creatures. They have produced a well-written and informative booklet in both French and English called *Let's Talk Turtles!* which provides answers to questions such as: "Why should we care about turtles?", "How many eggs does a turtle lay?", "Why do turtles cross roads and highways?". Michèle's newest idea is to see TURTLE S.H.E.L.L establish a turtle rehabilitation facility to help injured turtles return to the wild. The group also plans to instruct interested people in turtle rescue.

Michèle's enthusiasm, passion, dedication and energy are clearly infectious. It takes a remarkable person to see a problem, take action and find a solution. She singlehandedly rounded up experts in the field, rallied community support and convinced politicians to have a heart. How many individuals have accomplished so much? Michèle has helped make the area that much safer for the gentle, slow-moving and very vulnerable turtle.

Index to Volume 117

Compiled by Leslie Cody

Abies amabilis, 213
balsamea, 72,532,590
balsamifera, 362
lasiocarpa, 40,44,61,353,362,566
Abietinaria abietina, 557
kincaidi, 561
pulchra, 559
thuiarioides, 561
Accipiter gentilis, 12,479
striatus, 12
Acer spp., 378
pensylvanicum, 535
rubrum, 185,436,469,532,590,622
saccharinum, 470
saccharum, 389,532,590,622
saccharum ssp. *nigrum*, 649
saccharum ssp. *saccharum*, 649
Acesta angolensis, 440
bullisi, 440
columbiana, 440
excavata, 440
Acesta excavata (Bivalvia: Pectinoidea: Limidae), in the Northwest Atlantic, First record of the European Giant File Clam, 440
Achillea millefolium, 198,260
Acipenser fulvescens, 541
oxyrynchus, 59
Acipenser fulvescens, in a Natural Reach of the Ottawa River, Movement of Lake Sturgeon, 541
Aconitum delphinifolium ssp. *paradoxum*, 278
Actaea pachypoda, 650
rubra, 650
Actinemys, 415
Actitis macularia, 13
Adams, J.D., 415
Adiantum pedatum, 650
Adoxa moschatellina, 278,448
Aechmophorus occidentalis, 11
Aegolius acadicus, 14
funereus, 14
Aethia cristatella, 14
psittacula, 13
Agelaius phoeniceus, 16,169
tricolor, 311
XAgrohordeum macounii, 283
Agropyron cristatum, 168
dasystachum, 262
intermedium, 283
pectiniforme, 280
sibiricum, 280
smithii, 25,168,262
subsecundum, 262
Agrostis alba, 168
borealis, 452
capillaris, 536
exarata, 278
gigantea, 280
mertensii ssp. *mertensii*, 278,448
palustris, 536
scabra, 535
scabra var. *geminata*, 278
stolonifera, 536
tenuis, 536
Aix sponsa, 608
Alaska, A Northern Hawk Owl, *Surnia ulula*, Nest on a Man-made Structure in, 306
Alaska, Heavy Metal Concentrations in Arctic Foxes, *Alopex lagopus*, in the Prudhoe Bay Oil Field, 119
Albatross, Black-footed, 11
Alberta, Documenting Pronglorn Antelope, *Antilocapra americana*, in the Peace River Grasslands, 657
Alberta, Northern Harrier, *Circus cyaneus*, Attacks on Greater Sage-Grouse, *Centrocercus urophasianus*, in Southern, 479
Alberta, Seasonal Dynamics and Defoliation Impact on Herbage Yield in Aspen Boreal Habitats of, 196
Alces alces, 7,316,357,400,547,591
alces andersoni, 7
alces gigas, 7
Alder, Green, 203,290,455
Grey, 290
Sitka, 215
Speckled, 378,417
Aldridge, C.L., 479
Aldridge, C.L. and R.M. Brigham. Distribution, Abundance, and Status of the Greater Sage-Grouse, *Centrocercus urophasianus*, in Canada, 25
Alectoria, 39,44
ochroleuca, 66
sarmentosa, 39,46,62,354
Alewife, 59
Alfalfa, Yellow, 459
Alldredge, A.W., 316
Allium tricoccum, 650
Alnus crispa, 203,215,448
crispa ssp. *crispa*, 278
incana, 417
incana ssp. *tenuifolia*, 178
rubra, 213
rugosa, 378
Alopecurus geniculatus, 278
Alopex lagopus, 119,424,430
Alopex lagopus, Energy Cost of Running in an Arctic Fox, 430
Alopex lagopus, in the Prudhoe Bay Oil Field, Alaska, Heavy Metal Concentrations in Arctic Foxes, 119
Alosa pseudoharengus, 59
sapidissima, 59
Alvo, R. and S. Ponomarenko. Vegetation Classification Standard for Canada Workshop: 31 May–2 June 2000, 125
Amanita, 380

Ambrosia psilostachya, 645
Ambystoma jeffersonianum, 19
Ammodramus maritimus, 654
nelsoni, 169
Ammodytes hexapterus, 53
Amphibian Voice, 166,677
Amphicarpa bracteata, 650
Amphipacifica: Journal of Aquatic Systematic Biology 3(3), 164
Anas acuta, 12,605
americana, 11
clypeata, 12
crecca, 12
cyanoptera, 12
discors, 12,227,314
penelope, 11
platyrhynchos, 11,254
rubripes, 11
strepera, 11,608
Anas acuta, Initiate Rapid Follicular Growth During Spring Migration?, Do Female Northern Pintails, 605
Anderson, E.M., 419
Anderson, S.H., 308
Andromeda polifolia, 278
Andropogon gerardii, 218
hallii, 645
Androsace septentrionalis, 262
Anemone acutiloba, 650
canadensis, 103
multifida, 278
patens, 260
Anemone, Cut-leaf, 291
Angelica lucida, 449
Angelica, Seacoast, 461
Anguilla rostrata, 59
Anser albifrons, 11
Antelope, *Antilocapra americana*, in the Peace River Grasslands, Alberta, Documenting Pronglorn, 657
Antelope, Pronglorn, 657
Antennaria rosea ssp. *confinis*, 278
Anthus rubescens, 15
Antilocapra americana, 309,657
Antilocapra americana, in the Peace River Grasslands, Alberta, Documenting Pronglorn Antelope, 657
Aoki, K.A.A. and R.A. Bodaly. Sympatric Presence of Low and High Gillraker Forms of Cisco, *Coregonus artedi*, in Lake Athapapuskow, Manitoba, 49
Apargidium, 214
Aphelocoma californica, 311
Aphriza virgata, 13
Apocynum cannabinum var. *glaberrimum*, 449
sibiricum, 462
Apodemus sylvaticus, 245
Applegate, D.R., 122
Applegate, R.D., 645
Applegate, R.D. and D.R. Applegate. Winter Occurrence of Harlan's, *Buteo jamaicensis harlani*, and Krider's, *B. j. borealis*, Hawks in Eastern Kansas, 122
Aptenodytes forsteri, 231,430
Aquadro, C.F., 184
Aquila chrysaetos, 12,31,479,566
Aquilegia formosa, 278
Arabis boivinii, 278
codyi, 278
holboellii var. *retrofracta*, 279
kamtschatica, 279
Aralia spp., 594
Arceuthobium campylopodum, 306
Archibold, O.W., E.A. Ripley, and L. Delanoy. Effects of Season of Burning on the Microenvironment of Fescue Prairie in Central Saskatchewan, 257
Arcoscalpellum mitchellotianum, 441
Arctagrostis latifolia, 449
Arctanthemum integrifolium, 66
Ardea alba, 11
herodias, 11,603
Arenaria interpres, 13
melanocephala, 13
Arnica angustifolia ssp. *attenuata*, 279
chamissonis ssp. *chamissonis*, 279
griscomii ssp. *frigida*, 279
Arnica, Alpine, 299
Meadow, 299
Aronia melanocarpa, 395
Arrowhead, 168
Arsenault, A., 61
Artemisia borealis, 463
campestris, 449
cana, 25
dracunculus, 279
filifolia, 645
frigida, 25,262
ludoviciana, 258
tilesii, 449
Arthurs, W., Review by, 669
Ash, Black, 590
Green, 218
White, 649
Asio flammeus, 14,466
Aspen, 362,582
Largetooth, 436
Trembling, 76,91,196,378,395,436,590,652
Aspen Boreal Habitats of Alberta, Seasonal Dynamics and Defoliation Impact on Herbage Yield in, 196
Asphodel, Sticky False, 213
Aster falcatus, 258
laevis, 103,258
modestus, 279
sagittifolius, 198
sibiricus, 449
spathulatus, 449
umbellatus, 538
Aster, 258,463
Arctic, 463
Western Bog, 299
Astragalus aboriginum, 459
australis, 449
bodinii, 279
cicer, 280
goniatus, 262
tenellus, 279
Athyrium filix-femina var. *angustum*, 650
Atkinson, J., Reviews by, 158,508,674
Auditor's Report, 518
Auklet, Cassin's, 13
Crested, 14
Parakeet, 13
Rhinoceros, 14
Aulacomnium turgidum, 66
Aulichnites, 578

Avens, Hooker's Mountain, 294
Three-flowered, 258
Awlwort, 294,458
Aythya affinis, 12,582
americana, 12
collaris, 12,585,608
marila, 12,582
valisineria, 12,608
Aythya affinis, Reproductive Rates Declined in Parkland Manitoba?, Have Lesser Scaup, 582
Azalea, False, 214

Badger, 308
American, 348
Eurasion, 243
Bailey, M., Review by, 660
Balanus improvisus, 555
Ballard, W.B., 424,468,645
Ballard, W.B., M.A. Cronin, M.D. Robards, and W.A. Stubblefield. Heavy Metal Concentrations in Arctic Foxes, *Alopex lagopus*, in the Prudhoe Bay Oil Field, Alaska, 119
Baneberry, Red, 650
White, 650
Bartramia longicauda, 13
Basswood, 590
American, 650
Bat, Big Brown, 652
Eastern Red, 651
Hoary, 652
Little Brown, 17,652
Silver-haired, 652
Bat, *Lasiurus borealis*, from Cypress Hills Provincial Park, Saskatchewan: A Response to Climate Change?, New Records of the Eastern Red, 651
Bear, American Black, 18
Black, 113,193,407,566,591,621,626
Brown, 242
Florida Black, 113
Grizzly, 18,566
Louisiana Black, 113
North American Black, 236
Plains Grizzly, 30
Polar, 433,648
Svalbard Polar, 120
Bear, *Ursus americanus*, Denning Chronology and Den Site Selection in the Northeastern Cascades of Washington, Black, 626
Bear, *Ursus maritimus*, in northeast Saskatchewan, Extralimital Sighting of a Polar, 648
Bears, *Ursus americanus*, Associated with Elevated Train Trestles, Mortality of Black, 113
Bears, *Ursus americanus*, in Difficult Locations, Methods for Capturing Free-Ranging, 621
Bears, *Ursus americanus*, Phenotypic Variation in Skull Size and Shape Between Newfoundland and Mainland Populations of North American Black, 236
Beaudoin, A.B., Review by, 670
Beaver, 115,192,365,378,590
American, 17
Bedstraw, Northern, 258
Small, 298
Beech, 185,394,538,590
American, 389
Beggarticks, Nodding, 299
Bélanger, L., 167
Belant, J.L. and S.K. Windels. Small Mammal Abundance and Diversity in Forests with and without Canada Yew, *Taxus canadensis*, 389
Bell, Yellow, 304
Bellwort, Large-flowered, 650
Bennett, B., 278
Bennett, R., Review by, 674
Bergenske, J., 352
Bernier, C., 190
Betula spp., 395
alleghaniensis, 532,590
cordifolia, 532
glandulosa, 203,307
lenta, 622
neoalaskana, 279
occidentalis, 279
papyrifera, 61,279,362,378,532,590
pendula, 393
populifolia, 393
Betula pendula, on the Hydrology of Wainfleet Bog, Ontario, Lack of Evidence for Impact of the European White Birch, 393
Bidens cernua, 279
Bider, J.R., 377
Bimeria brevis, 561
Birch, 395
Alaska, 290
Black, 622
Bog, 307
Dwarf, 203
European White, 393
Mountain, 532
Paper, 290,362
Water, 290
White, 378,532,590
Yellow, 532,590
Birch, *Betula pendula*, on the Hydrology of Wainfleet Bog, Ontario, Lack of Evidence for Impact of the European White, 393
Bishop's Cap, Two-leaved, 650
Bison bison, 18,657
Bison, 657
American, 7
Bitterbrush, 628
Bitter-cress, Little Western, 292
Bittern, American, 11
Blackbird, Red-winged, 7,169
Rusty, 16
Tricolored, 311
Bladderpod, Arctic, 294
Bladderwort, Lesser, 298
Blarina brevicauda, 246,390
Blechnum spicant, 211
Blue-joint, 282
Blueberry, Bog, 213
Oval-leaved, 461
Bluebird, Mountain, 7,110
Bluebirds, *Sialia currucoides*, and Tree Swallows, *Tachycineta bicolor* with Monthly Air Temperatures, Comparison of Spring Return Dates of Mountain, 110
Bluegrass, 196
Bog, 285
Canada, 285
Kentucky, 168,196,258

Rough, 285
Sandberg, 285
Bluestem, Big, 218
Little, 218
Old World, 425
Sand, 645
Bobcat, 193,361,472
Bobcats, *Lynx rufus*, and Raccoons, *Procyon lotor*, Relative to Home Range Boundaries, Capture Locations of Coyotes, *Canis latrans*, 472
Bobolinks, 169
Bodaly, R.A., 49
Boertmann, D. Distribution and Conservation of the Harlequin Duck, *Histrionicus histrionicus*, in Greenland, 249
Bog-laurel, 296
Boles, S.R., 469
Boletus, 380
Bombycilla cedrorum, 15,177
garrulus, 15
Bonasa umbellus, 12,177,313,365
Boreal Dip Net: Newsletter of the Canadian Amphibian and Reptile Conservation Network, *The*, 343
Bork, E.W., 196
Botaurus lentiginosus, 11
Bothriochloa spp., 425
Botrychium lunaria, 449
Bougainvillia sp., 557
Bourgeois, J.-C., 377,605
Bousfield, E.L., 140
Bouteloua curtipendula, 218,425
gracilis, 25,425,645
Brachyramphus brevirostris, 13
marmoratus, 13,53
Bramble, Five-leafed, 214
Brambling, 16
Brant, 11
Branta bernicla, 11
canadensis, 11,227
Breton, L., 399,546
Brigham, R.M., 25,651
British Columbia, and its Palaeobotanical Implications, An Occurrence of the Hawkweed-Leaved Saxifrage, *Saxifraga hieraciifolia*, in Southern, 304
British Columbia, Bald Eagles, *Haliaeetus leucocephalus*, Feeding on Spawning Plainfin Midshipman, *Porichthys notatus*, at Crescent Beach, 601
British Columbia, Characteristics of Early-Winter Caribou, *Rangifer tarandus caribou*, Feeding Sites in the Southern Purcell Mountains, 352
British Columbia Coast, The Shoreline Fringe Forest and Adjacent Peatlands of the Southern Central, 209
British Columbia, Notes on the *Populus* "Dripzone Effect" on Lichens in Well-ventilated Stands in East-central, 61
British Columbia, Seasonal Habitat Use and Movements of Mountain Goats, *Oreamnos americanus*, in East-central, 565
British Columbia, Sightings of Vagrant Pacific Alcids in Desolation Sound, 53
Brome, California, 282
Smooth, 168,197
Bromegrass, 196
Smooth, 196
Bromus carinatus, 280
inermis, 168,196
secalinus, 536
Brooks, R.T., 190
Browning, M., 393
Brunjes, J.H. IV and W.D. Webster. Marsh Rice Rat, *Oryzomys palustris*, Predation on Forster's Tern, *Sterna forsteri*, Eggs in Coastal North Carolina, 654
Brunton, D.F. A Tribute to Clarence Frankton 1906-2000, 481
Bryoria spp., 39,44,352
capillaris, 45,62
chalybeiformis, 45
fremontii, 39,45
fuscescens, 39,45,62
glabra, 39,45
implexa, 45
lanestris, 45
pseudofuscescens, 39,45
simplicior, 45
tortuosa, 45
(*Bryoria*) in High-Elevation Oldgrowth Conifer Forests, On the Dispersal of Hair Lichens, 44
(*Bryoria*) in the Canopies of High-elevation Oldgrowth Conifer Forests, On the Vertical Zonation of Hair Lichens, 39
Bubo virginianus, 14,227,479
Bucephala albeola, 12
clangula, 12
islandica, 12
Buchloe dactyioides, 425,645
Buckbean, 297,436,462
Buckleberry, 352
Budworm, Spruce, 531
Buffalograss, 425
Bufflehead, 12
Bufo americanus, 380,477
Bugseed, 455
Bulrush, 103
Common Great, 453
Hardstem, 226
Bunchberry, 214,352
Bunting, Snow, 7,177
Bur-reed, Giant, 168
Small, 281
Burbot, 59
Burke, A.M. Sandhill Crane, *Grus canadensis*, Nesting in the Yorkton Wetland Complex, Saskatchewan, 224
Burnet, Canadian, 295
Great, 213
Bush, Flowering, 103
Buteo jamaicensis, 12,122,179,479
jamaicensis borealis, 122
jamaicensis harlani, 122
lagopus, 12
regalis, 479
swainsoni, 12,479
Buteo jamaicensis borealis, Hawks in Eastern Kansas, Winter Occurrence of Harlan's, *Buteo jamaicensis harlani*, and Krider's, 112
Buteo jamaicensis harlani, and Krider's, *B. j. borealis*, Hawks in Eastern Kansas, Winter Occurrence of Harlan's, 122
Butomus umbellatus, 103
Butter-and-eggs, 298
Buttercup, Birdfoot, 292

Dwarf, 457
Pallas', 457
Snow, 457
Subalpine, 292
Sulpher, 457
White Water, 292
Butterweed, Rayless Mountain, 299

Cabanac, A.J. Physical Condition of an Animal, Using as an Example the Common Eider, *Somateria mollissima*, 230
Cabbage, Deer, 213
Cadorette, S., Review by, 662
Calamagrostis canadensis, 168,535
canadensis ssp. *canadensis*, 279
canadensis ssp. *langsdorfii*, 279
purpurascens var. *purpurascens*, 279
stricta ssp. *inexpansa*, 279
Calamovilfa longifolia, 645
Calcarius lapponicus, 16
pictus, 16
Calder, D.R. Subtidal Hydroids (Cnidaria) of Northumberland Strait, Atlantic Canada, with Observations on Their Life Cycles and Distributions, 555
Calidris alba, 13
alpina, 13
bairdii, 13
canutus, 13
mauri, 13
melanotos, 13
minutilla, 13
ptilocnemis, 13
pusilla, 13
ruficollis, 13
Caligus clemensi, 634
Caloplaca holocarpa, 62
Caltha natans, 449
palustris ssp. *arctica*, 449
Calycella syringa, 557
Calypte anna, 14
Calyptospadix cerulea, 561
Campanula rotundifolia, 260
Campanularia gelatinosa, 561
groenlandica, 557
hincksii, 561
volubilis, 559
Campbell, C.E., 477
Campbell, G.D., 589
Campion, Arctic, 291
Bladder, 260
Moss, 291
Taimyr, 291
Canada*, A Review of the Canada Lynx, *Lynx canadensis*, in, 360
Canada, Distribution, Abundance, and Status of the Greater Sage-Grouse, *Centrocercus urophasianus*, in, 25
Canada, *Dryopteris goldiana* × *D. intermedia*, a Natural Fern Hybrid New to, 649
Canada Lynx, *Lynx canadensis*, in Canada*, A Review of the, 360
Canada, *Malaxis monophyllos* var. *brachypoda*, One-leaved Malaxis, new to the Northwest Territories, 302
Canada, Patterns of Nestling Feeding in Harris's Sparrows, *Zonotrichia querula* and White-crowned Sparrows, *Z. leucophrys*, in the Northwest Territories, 203
Canada, Supposed Periodicity of Redpoll, *Carduelis* sp., Winter Visitations in Atlantic, 611
Canada, II, Additions and Range Extensions to the Vascular Plant Flora of the Continental Northwest Territories and Nunavut, 448
Canada, with Observations on Their Life Cycles and Distributions, Subtidal Hydroids (Cnidaria) of Northumberland Strait, Atlantic, 555
Canada Workshop: 31 May–2 June 2000, Vegetation Classification Standard for, 125
Canada Yew, *Taxus canadensis*, Small Mammal Abundance and Diversity in Forests with and without, 389
Canadian Atlantic Ichthyofauna, The Chain Dogfish, *Scyliorhinus retifer* (Garman, 1881), New to the, 475
Canadian Field-Naturalist, Advice for Contributors to *The*, 522
Canadian Species at Risk, 166,513
Canis familiaris, 123,380
Canis latrans, 17,30,123,242,308,364,468,472,645
latrans-lupus, 589
lupus, 17,30,120,242,357,364,400,419,468,469,550,566
lupus ligoni, 7
lupus nubilus, 7
lupus occidentalis, 7
lupus X *latrans*, 589
lupus-lycaon, 589
lycaon, 589
mesomelas, 424
rufus, 589
Canis familiaris, Kill Coyote, *Canis latrans*, Feral Dogs, 123
Canis latrans, Bobcats, *Lynx rufus*, and Raccoons, *Procyon lotor*, Relative to Home Range Boundaries, Capture Locations of Coyotes, 472
Canis latrans, Feral Dogs, *Canis familiaris*, Kill Coyote, 123
Canis latrans – Rio Grand Turkey, *Meleagris gallopavo intermedia*, interactions, Coyote, 645
Canis lupus, in Porcupine, *Erethizon dorsatum*, Dens in Wisconsin, Death of Gray Wolves, 469
Canis lupus, Pack Structure: Conservation Implications for Recovering Populations, Limits to Plasticity in Gray Wolf, 419
Canis lupus × *latrans* Hybrid Zone, Southeastern Ontario, Landscape Influence on *Canis* Morphological and Ecological Variation in a Coyote-Wolf, 589
Canvasback, 12,608
Capelin, 70
Capreolus capreolus, 242
Cardamine oligosperma ssp. *kamtschatica*, 292
umbellata, 279
Cardinal, Northern, 177
Cardinalis cardinalis, 177
Carduelis sp., 611
flammea, 16,611
hornemanni, 16,611
pinus, 16,177
tristis, 179
Carduelis sp., Winter Visitations in Atlantic Canada, Supposed Periodicity of Redpoll, 611
Carex spp., 103,210
arcta, 279,449
atherodes, 103,279
atrofusca, 279
bicolor, 279
bonanzensis, 279
brunnescens, 279

buxbaumii, 279
capillaris ssp. *capillaris*, 279
concinna, 279
deflexa, 279
disperma, 449
eleocharis, 262
eleusinoides, 279
filifolia, 197
flava, 279
franklinii, 279
garberi ssp. *bifaria*, 279
glacialis, 279
heliophila, 258
hoodii, 448
lanuginosa, 103
leporina, 536
magellanica ssp. *irrigua*, 279
maritima, 449
media, 279
microglochin, 279
microptera, 448
misandra, 67
nardina, 67
obtusata, 258,279
pachystachya, 279
pauciflora, 214
pedunculata, 650
petasata, 448
phaeocephala, 279
plantaginea, 650
platyphylla, 650
rostrata, 103,279
scirpoidea, 67
tenuiflora, 449
trisperma, 537
viridula, 279
williamsii, 279
Caribou, 18,120,253,399
Barren-ground, 7,39
Mountain, 39,44,356
Woodland, 7,39,44,352,546
Caribou, *Rangifer tarandus caribou*, An Aerial Survey Technique for the Forest-Dwelling Ecotype of Woodland, 546
Caribou, *Rangifer tarandus caribou*, Feeding Sites in the Southern Purcell Mountains, British Columbia, Characteristics of Early-Winter, 352
Caribou, *Rangifer tarandus*, in Quebec, Historical Changes and Current Distribution of, 399
Carlson, J., W.A. Gough, J.D. Karagatzides, and L.J.S. Tsuji. Canopy Interception of Acid Deposition in Southern Ontario, 523
Carpodacus purpureus, 16
Carya spp., 19,622
cordiformis, 218,649
Cassiope mertensiana, 354
tetragona, 66
Castilleja caudata, 298
pallida var. *caudata*, 279
Castor canadensis, 17,115,192,365,378,590
Cat, Domestic, 380
Feral, 380
Catastomous catostomous, 59
Cathartes aura, 11
Catharus guttatus, 15
minimus, 15
ustulatus, 15
Catling, P.M. *Dryopteris goldiana* × *D. intermedia*, a Natural Fern Hybrid New to Canada, 649
Catostomous commersoni, 59
Cattail, 103,168
Caulophyllum thalictroides, 650
Cedar, Eastern White, 590
Western Red, 214
White, 470
Yellow, 213
Celtis occidentalis, 218
Centrocercus spp., 25
urophasianus, 25,308,479
Centrocercus urophasianus, in Canada, Distribution, Abundance, and Status of the Greater Sage-Grouse, 25
Centrocercus urophasianus, in Southern Alberta, Northern Harrier, *Circus cyaneus*, Attacks on Greater Sage-Grouse, 479
Centrocercus urophasianus, Nest Predators Using Remote Sensing Cameras, Direct Identification of Northern Sage-grouse, 308
Cephaloziella spp., 535
Cepphus columba, 13,54
Cerastium alpinum, 67
arvense, 260,279
Ceratophyllum demersum, 279
Cerorhinca monocerata, 14
Certhia americana, 15,177
Cervus elaphus, 196,309,357
elaphus nelsoni, 316
Cervus elaphus nelsoni, During the Calving Season Toward Mule Deer, *Odocoileus hemionus*, in Central Colorado, Aggressive Interactions of Rocky Mountain Elk, 316
Ceryle alcyon, 14
Chaetura vauxi, 14
Chamaecyparis nootkatensis, 212
Chamaedaphne calyculata, 436,449
Chamberlain, M.J., 113
Chamerion latifolium, 67
Char, Arctic, 59,254,634
Chara spp., 273
Charadrius semipalmatus, 12
vociferus, 11,311
Chardine, J.W., 70
Chelydra serpentina serpentina, 415
Chen caerulescens, 11,226
caerulescens atlantica, 608
caerulescens caerulescens, 608
canagica, 11
Cherry, Black, 19,395
Chickadee, Black-capped, 15,179
Boreal, 15
Chestnut-backed, 7
Gray-headed, 15
Mountain, 15,76
Chickadees, *Poecile gambeli*, to Playback of Different Song Types, Response of Male Mountain, 76
Chickweed, 291
Field, 260,290
Long-leaved, 291
Chiloscyphus spp., 535
Chinook, 639
Chipmunk, Eastern, 246,591
Least, 7,309

Chlidonias niger, 13
Choke-cherry, 417
Chondestes grammacus, 16
Chordeiles minor, 14
Chorilia longipes, 118
Choristoneura fumiferana, 531
Chrysanthemum integrifolium, 66,279,449
leucanthemum, 536
Chrysemys picta picta, 415
Chrysosplenium tetrandrum, 449
Chrysothamnus sp., 645
Chub, Lake, 59
Chum, 638
Cicuta maculata var. *angustifolia*, 279
Cinclus mexicanus, 15
Cinna latifolia, 279
Cinquefoil, Snow, 295
Three-toothed, 459
White, 260
Circaea alpina ssp. *alpina*, 279
Circus cyaneus, 12,227,479
Circus cyaneus, Attacks on Greater Sage-Grouse, *Centrocercus urophasianus*, in Southern Alberta, Northern Harrier, 479
Cirriped, Stalked, 441
Cirsium spp., 103
arvense, 198,536
vulgare, 536
Cisco, 49
Shortjaw, 49,642
Cisco, *Coregonus artedi*, in Lake Athapapuskow, Manitoba, Sympatric Presence of Low and High Gillraker Forms of, 49
Cistothorus palustris, 169,348,654
Cladina mitis, 66
Cladonia spp., 352,535
Cladonia, 352
Clam, *Acesta excavata* (Bivalvia: Pectinoidea: Limidae), in the Northwest Atlantic, First record of the European Giant File, 440
Clam, European Giant File, 440
Clangula hyemalis, 12,254
Clava leptostyla, 561
multicornis, 561
Clemmys, 415
guttata, 436
insculpta, 377
Clemmys guttata, Near their Northern Limit: an 18-Year Follow-up, Population Structure, Growth, and Age Estimation of Spotted Turtles, 436
Clethrionomys spp., 246,348
gapperi, 246,390
rutilus, 17
Clover, 168
Red, 296
White, 197
White Sweet, 459
Club-moss, Alpine, 280
Common, 280,450
Flatbranch, 280,450
Running, 214
Clubrush, Tufted, 213,288
Clytia hemisphaerica, 559
Coad, B.W., 475
Coad, B.W., Reviews by, 151,318,319,323,324
Coccothraustes vespertinus, 177
Cody, W.J., Reviews by, 329,330,496,669
Cody, W.J. and V. Johnston. *Malaxis monophyllos* var. *brachypoda*, One-leaved Malaxis, new to the Northwest Territories, Canada, 302
Cody, W.J., C.E. Kennedy, B. Bennett, and J. Staniforth. New Records of Vascular Plants in the Yukon Territory V, 278
Cody, W.J., K.L. Reading, and J.M. Line. Additions and Range Extensions to the Vascular Plant Flora of the Continental Northwest Territories and Nunavut, Canada, II, 448
Coelopleurum gmelinii, 461
Coho, 638
Cohosh, Blue, 650
Colaptes auratus, 14
Colorado, Aggressive Interactions of Rocky Mountain Elk, *Cervus elaphus nelsoni*, During the Calving Season Toward Mule Deer, *Odocoileus hemionus*, in Central, 316
Coltsfoot, Arrow-leaved, 464
Sweet, 464
Columba fasciata, 14
livia, 14,176
Columbine, Western, 291
Comandra umbellata ssp. *pallida*, 279
Comandra, Pale, 290
Contopus cooperi, 14
sordidulus, 14
Cook, F.R., Reviews by, 490,491,492,493,494,495,509
Cooke, S.J., Reviews by, 156,499
Coot, American, 12
Coral, 440
Corallorhiza trifida, 449
Coralroot, Yellow, 454
Cordgrass, Smooth, 654
Cordylophora caspia, 561
lacustris, 561
Coregonus, 49
artedi, 49
clupeaformis, 59,642
zenithicus, 49,642
Coregonus artedi, in Lake Athapapuskow, Manitoba, Sympatric Presence of Low and High Gillraker Forms of Cisco, 49
Corispermum hookeri, 448
ochotense, 448
orientale var. *emarginatum*, 455
villosum, 448
Cormorant, Double-crested, 11
Pelagic, 11
Cornus canadensis, 211,352,535
Corvus brachyrhynchos, 30,227
caurinus, 15,602
corax, 15,30,227,308
Corymorpha pendula, 558
Cosgrove, J.A. An *in situ* Observation of Webover Hunting by the Giant Pacific Octopus, *Enteroctopus dofleini* (Wülker, 1910), 117
Cotton-grass, 395
Arctic, 288
Scheuchzer's, 288
Short-anthered, 287
Cottontail, 314
Eastern, 591,645

Cottus bairdi, 59
cognatus, 59
Coturnix japonica, 348
Couesius plumbeus, 59
Cougar, 7,357,566
Courtois, R., A. Gingras, C. Dussault, L. Breton and J.-P. Ouellet. An Aerial Survey Technique for the Forest-Dwelling Ecotype of Woodland Caribou, *Rangifer tarandus caribou*, 546
Courtois, R., J.-P. Ouellet, A. Gingras, C. Dussault, L. Breton and J. Maltais. Historical Changes and Current Distribution of Caribou, *Rangifer tarandus*, in Quebec, 399
Couture, R., 605
Cow, Domestic, 309
Cowbird, Brown-headed, 16,348
Coyote, 17,30,123,227,242,308,364,468,472,645
Coyote, *Canis latrans*, Feral Dogs, *Canis familiaris*, Kill, 123
Coyote, *Canis latrans* – Rio Grand Turkey, *Meleagris gallopavo intermedia*, interactions, 645
Coyote-Wolf, 589
Coyote-Wolf, *C. lupus* × *latrans* Hybrid Zone, Southeastern Ontario, Landscape Influence on *Canis* Morphological and Ecological Variation in a, 589
Coyotes, *Canis latrans*, Bobcats, *Lynx rufus*, and Raccoons, *Procyon lotor*, Relative to Home Range Boundaries, Capture Locations of, 472
Crab, 117
Crab-Apple, Pacific, 215
Craig, T., 306
Cranberry, Bog, 213,461
Large, 436
Small, 436
Crane, Sandhill, 12,224
Whooping, 224
Crane, *Grus canadensis*, Nesting in the Yorkton Wetland Complex, Saskatchewan, Sandhill, 224
Crassostrea virginica, 555
Crassula aquatica, 449
Crataegus sp., 311
Creeper, Brown, 7,177
Crepis tectorum, 448
Cress, Garden, 294
Crocus, Prairie, 260
Cronin, M.A., 119
Crossbill, Red, 16
White-winged, 16
Crow, American, 30,227
Northwestern, 7,602
Crowberry, 213
Curatorial Reports on Natural History Topics: Nova Scotia Museum of Natural History, 165
Curlew, Bristle-thighed, 13
Cuspidella humilis, 557
Cyanocitta cristata, 179,193
stelleri, 15
Cyclopterus lumpus, 254
Cygnus buccinator, 11
columbianus, 11
Cyperus esculentus, 106
rotundus, 106
Cystophora cristata, 121
Cystopteris fragilis, 279,449
montana, 279,449
Dace, Longnose, 57
Pearl, 59
Dace, *Rhinichthys cataractae*, in Newfoundland and Labrador, Range Extensions of Logperch, *Percina caprodes*, and Longnose, 57
Dactylis glomerata, 278
Daigle, C., 377
Daisy, Entire-leaved, 66,299,463
Daisy, *Hulteniella integrifolia* (Asteraceae), in Québec, Eco-geographical and Cytological Notes on the Entire-leaved, 66
Danby, R.K. Birds and Mammals of the St. Elias Mountain Parks: Checklist Evidence for a Biogeographic Convergence Zone, 1
Dandelion, 197
Danthonia intermedia, 449
spicata, 448
Davies, J.-A., 352
Deer, European Roe, 242
Mule, 7,309,316,357,657
Red, 309
White-tailed, 309,316,357,389,407,567,590
Deer, *Odocoileus hemionus*, in Central Colorado, Aggressive Interactions of Rocky Mountain Elk, *Cervus elaphus nelsoni*, During the Calving Season Toward Mule, 316
DeGraaf, R.M., 190
Delanoy, L., 257
Delphinium glaucum, 279
Dendragapus obscurus, 12
Dendranthema integrifolium, 66
Dendroica caerulescens, 389
coronata, 15
palmarum, 15
petechia, 15,206,309
striata, 15
townsendi, 15
Dennstaedtia punctilobula, 535
Deparia acrostichoides, 650
Deschampsia elongata, 448
Descurainia incisa var. *incisa*, 448
sophioides, 279
Desmognathus fuscus, 19
ochrophaeus, 19
Diamond, J., M. Browning, A. Williams, and J. Middleton. Lack of Evidence for Impact of the European White Birch, *Betula pendula*, on the Hydrology of Wainfleet Bog, Ontario, 393
Dicoryne conferta, 558
Dicranum sp., 214
elongatum, 66
ontariense, 535
Dicrostonyx, 466
Dignard, N. and C. Gervais. Eco-geographical and Cytological Notes on the Entire-leaved Daisy, *Hulteniella integrifolia* (Asteraceae), in Québec, 66
Dion, N., K.A. Hobson and S. Larivière. Does Removal of Duck Nest Predators Affect the Temporal Patterns of Predation for Simulated Nests of Grassland Songbirds?, 347
Diphasia fallax, 557
kincaidi, 561
Diplazium pycnocarpon, 650
Dipper, American, 15
Dobony, C.A., 313

Dock, Western, 103
Dockrill, C.W., 479
Dodecatheon pulchellum, 304
Dog, 380
Feral, 123
Dogbane, Common, 462
Dogfish, Chain, 475
Dogfish, *Scyliorhinus retifer* (Garman, 1881), New to the Canadian Atlantic Ichthyofauna, The Chain, 475
Dogs, *Canis familiaris*, Kill Coyote, *Canis latrans*, Feral, 123
Dolichonyx oryzivorus, 169
Dombrowski, P., J.-C. Bourgeois, R. Couture, and C. Linard. Do Female Northern Pintails, *Anas acuta*, Initiate Rapid Follicular Growth During Spring Migration?, 605
Donkor, N.T., M.M. Okello, R.J. Hudson and E.W. Bork. Seasonal Dynamics and Defoliation Impact on Herbage Yield in Aspen Boreal Habitats of Alberta, 196
Doolittle, C.J.T., 469
Dove, Mourning, 14,177
Rock, 14,176
Dowitcher, Long-billed, 13
Short-billed, 13
Draba albertina, 279
alpina, 449
borealis, 279
cana, 279
cinerea, 279,449
glabella, 449
incerta, 279
kananaskis, 278,293
lactea, 449
macounii, 279
porsildii, 279
scotteri, 279
stenoloba, 448
Draba, Alpine, 457
Macoun's, 294
Northern, 293
Slender, 293
Dropseed, 645
Sand, 425
Drosera rotundifolia, 213
Drury, C.F., 267
Dryas crenulata, 279
hookeriana, 279
integrifolia, 66
Dryopteris campyloptera, 535
carthusiana, 651
celsa, 650
clintoniana, 650
clintoniana × *goldiana*, 651
correllii, 651
cristata, 650
disjuncta, 451
expansa, 279
goldiana, 649
goldiana × *intermedia*, 651
intermedia, 649
marginalis, 390
× *mickelii*, 651
spinulosa, 535
Dryopteris goldiana × *D. intermedia*, a Natural Fern Hybrid New to Canada, 649
Dryopteris intermedia, a Natural Fern Hybrid New to Canada, *Dryopteris goldiana* ×, 649
Duck, American Black, 11
Harlequin, 12,249
Long-tailed, 7,254
Ring-necked, 7,585,608
Ruddy, 12
Wood, 608
Duck, *Histrionicus histrionicus*, in Greenland, Distribution and Conservation of the Harlequin, 249
Dunlin, 13
Dussault, C., 399,546
Dynamena pumila, 561

Eagle, Bald, 12,601
Golden, 12,31,479,566
Eagles, *Haliaeetus leucocephalus*, Feeding on Spawning Plainfin Midshipman, *Porichthys notatus*, at Crescent Beach, British Columbia, Bald, 601
Ectopleura crocea, 561
larynx, 558
Editor's Report for Volume 116 (2002), 345
Edwards, J.W., 313
Edwards, M.A. and G.J. Forbes. Food Habits of Ermine, *Mustela erminea*, in a Forested Landscape, 245
Eedy, W., Reviews by, 160,342
Eel, American, 59
Eelgrass, 655
Egret, Great, 11
Eider, Common, 12,230,608
King, 12
Eider, *Somateria mollissima*, Physical Condition of an Animal, Using as an Example the Common, 230
Elderberry, Red, 538
Eleocharis acicularis, 449
pauciflora var. *fernaldii* 453
quinqueflora, 449
Elk, 357
American, 309
Rocky Mountain, 316
Elk, *Cervus elaphus nelsoni*, During the Calving Season Toward Mule Deer, *Odocoileus hemionus*, in Central Colorado, Aggressive Interactions of Rocky Mountain, 316
Elliott, J.E., 601
Elliott, K.H., C.L. Struik and J.E. Elliott. Bald Eagles, *Haliaeetus leucocephalus*, Feeding on Spawning Plainfin Midshipman, *Porichthys notatus*, at Crescent Beach, British Columbia, 601
Elm, American, 218
White, 590
X*Elyhordeum macounii*, 279
Elymus canadensis, 449
elongatus ssp. *ponticus*, 280
glaucus, 279
hispidus, 280
junceus, 278
macounii, 283
macrourus, 279
trachycaulus ssp. *andinus*, 279
trachycaulus ssp. *glaucus*, 279
trachycaulus ssp. *novae-angliae*, 279
trachycaulus ssp. *subsecundus*, 279
trachycaulus ssp. *trachycaulus*, 279
trachycaulus ssp. *violaceus*, 279

Elytrigia intermedia, 283
Empetrum nigrum, 211
Empidonax alnorum, 14
difficilis, 14
flaviventris, 14
hammondii, 14
minimus, 14
oberholseri, 14
Emydoidea blandingii, 415
Enhydra lutris, 3
Enteroctopus dofleini, 117
Enteroctopus dofleini (Wülker, 1910), An *in situ* Observation of Webover Hunting by the Giant Pacific Octopus, 117
Epilobium anagalidifolium, 449
angustifolium, 535
arcticum, 449
davuricum, 449
davuricum var. *arcticum*, 460
hornemannii, 279,449
leptophyllum, 449
palustre, 279,449
Eptesicus fuscus, 652
Equisetum arvense, 449
fluviatile, 103
palustre, 449
scirpoides, 449
variegatum, 449
variegatum ssp. *variegatum*, 279
Eragrostis trichodes, 645
Eremophila alpestris, 15
Erethizon dorsatum, 17,469
Erethizon dorsatum, Dens in Wisconsin, Death of Gray Wolves, *Canis lupus*, in Porcupine, 469
Erignathus barbatus, 121
Eriophorum angustifolium, 211
brachyantherum, 279
callitrix, 279
scheuchzeri, 279
vaginatum, 395
viridi-carinatum, 449
Eritrichium splendens, 279
Ermine, 18,193,245
Ermine, *Mustela erminea*, in a Forested Landscape, Food Habits of, 245
Erskine, A.J. and R. McManus, Jr. Supposed Periodicity of Redpoll, *Carduelis* sp., Winter Visitations in Atlantic Canada, 611
Erysimum cheiranthoides, 279
coarctatum, 448
Erythronium grandiflorum, 304
Esox lucius, 59
Eudendrium album, 558
dispar, 557
ramosum, 557
Eupatorium rugosum, 650
Euphagus carolinus, 16
Eutamias minimus, 309

Fagus, 394
grandifolia, 185,389,535,590
Falcipennis canadensis, 12
Falco columbarius, 12
peregrinus, 12
rusticolus, 12,479
sparverius, 12
tinnunculus, 424
Falcon, Peregrine, 12
Falsebox, 352
Fauria crista-galli, 211
Felis concolor, 18,357
domestica, 380
Felwort, Marsh, 462
Ferguson, T.A. Documenting Pronglorn Antelope, *Antilocapra americana*, in the Peace River Grasslands, Alberta, 657
Fern, Bracken, 214
Deer, 213
Evergreen Wood, 649
Fragile, 280,450
Goldie's, 649
Mountain Bladder, 281,450
Northern Lady, 650
Northern Maidenhair, 650
Northern Wood, 281
Oak, 281,451,650
Silvery Glade, 650
Fescue, Hard, 284
Mountain Rough, 89
Plains Rough, 89,258
Red, 168,284
Richardson's, 284
Tundra, 284
Fescue Prairie in Central Saskatchewan, Effects of Season of Burning on the Microenvironment of, 257
Festuca altaica, 262
altaica ssp. *hallii*, 258
campestris, 89
hallii, 89
lenensis, 279
richardsonii, 279
rubra, 168,279
tenuifolia, 536
trachyphylla, 280
Filellum serpens, 559
Filion, B., 167
Finch, Purple, 7
Fir, Balsam, 72,362,532,590
Douglas, 45,91,353,362,628
Subalpine, 40,44,353,362,566
Fireweed, 538
Fisher, 193,590
Flavocetraria nivalis, 66
Fletcher, Q.E., C.W. Dockrill, D.J. Saher, and C.L. Aldridge. Northern Harrier, *Circus cyaneus*, Attacks on Greater Sage-Grouse, *Centrocercus urophasianus*, in Southern Alberta, 479
Flicker, Northern, 14
Flycatcher, Alder, 14
Dusky, 7
Hammond's, 14
Least, 14
Olive-sided, 14
Pacific-slope, 7
Scissor-tailed, 14
Yellow-bellied, 14
Foamflower, 352
Fogfruit, 650
Forbes, G.J., 245
Ford, W.M., 313

Forget-me-not, Showy Alpine, 297
Fox, Arctic, 119,424,430
Gray, 468
Kit, 123,424,468
Red, 17,30,123,227,308,348,365,380,424,468,472,586, 591
Swift, 30,123,424,468
Fox, *Alopex lagopus*, Energy Cost of Running in an Arctic, 430
Fox, *Vulpes velox*, White Color Phase of the Swift, 468
Foxes, *Alopex lagopus*, in the Prudhoe Bay Oil Field, Alaska, Heavy Metal Concentrations in Arctic, 119
Foxes, *Vulpes velox*, in Northwestern Texas, Den Site Activity Patterns of Adult Male and Female Swift, 424
Fragaria sp., 380
virginiana ssp. *glauca*, 279
Frankton 1906-2000, A Tribute to Clarence, 481
Fratercula arctica, 70
cirrhata, 14
corniculata, 14
Fratercula arctica, in North America, Status of the Largest Breeding Concentration of Atlantic Puffins, 70
Fraxinus americana, 649
nigra, 590
pennsylvanica, 218
Freedman, B., 531
Fringilla montifringilla, 16
Fritillaria pudica, 304
Frog, Chorus, 477
Green, 477
Mink, 477
Northern Leopard, 477
Wood, 477
Frog, *Rana septentrionalis*, from Insular Newfoundland, First Record of Mink, 477
Froglog: Newsletter of the Declining Amphibian Populations Task Force, 164,343,513,677
Fuglei, E. and N.A. Oritsland. Energy Cost of Running in an Arctic Fox, *Alopex lagopus*, 430
Fulica americana, 12
Fuller, T.K., 190
Fulmar, Northern, 11
Fulmarus glacialis, 11
Fumagalli, L., 82

Gadwall, 7,608
Gagnon, J.-M. and R.L. Haedrich. First record of the European Giant File Clam, *Acesta excavata* (Bivalvia: Pectinoidea: Limidae), in the Northwest Atlantic, 440
Gaines, W.L. Black Bear, *Ursus americanus*, Denning Chronology and Den Site Selection in the Northeastern Cascades of Washington, 626
Gale, Sweet, 213
Galeopsis tetrahit, 103,536
Galium boreale, 258
trifidum, 279
Galliformes, ssp., 365
Gallinago gallinago, 13,169
Gardali, T. and J.D. White. Autumn and Winter Breeding Records for the American Robin, *Turdus migratorius*, 311
Garveia brevis, 561
franciscana, 555
Gasterosteus aculeatus, 59
Gaultheria shallon, 211
Gavia adamsii, 11
immer, 11,254
pacifica, 11
stellata, 11
Gawn, M., Review by, 322
Gehring, J.L., 419
Gehring, T.M., B.E. Kohn, J.L. Gehring, and E.M. Anderson. Limits to Plasticity in Gray Wolf, *Canis lupus*, Pack Structure: Conservation Implications for Recovering Populations, 419
Gentian, Spurred, 462
Gentiana propinqua, 462
Gentianella propinqua ssp. *propinqua*, 449
Geothlypis trichas, 16
Gervais, C., 66
Geum triflorum, 258
Gilhen, J., 415
Gilhen, J., B.W. Coad and A. Hebda. The Chain Dogfish, *Scyliorhinus retifer* (Garman, 1881), New to the Canadian Atlantic Ichthyofauna, 475
Gingras, A., 399,546
Ginns, J., Review by, 328
Gipson, P.S., 123,218,645
Gipson, P.S. and J.F. Kamler. Capture Locations of Coyotes, *Canis latrans*, Bobcats, *Lynx rufus*, and Raccoons, *Procyon lotor*, Relative to Home Range Boundaries, 472
Giroux, J.-F., 167
Glaucomys spp., 193,365
sabrinus, 17
Gleditsia triacanthos, 218
Glyptemys, 415
insculpta, 377,415
Glyptemys insculpta, at River Denys: A Second Population for Cape Breton Island, Nova Scotia, The Wood Turtle, 415
Glyptemys insculpta, Population at the Northern Limit of its Range in Québec, Ecological Aspects of a Wood Turtle, 377
Goat, Mountain, 7,565
Goats, *Oreamnos americanus*, in East-central British Columbia, Seasonal Habitat Use and Movements of Mountain, 565
Godfrey, 1910–2002, A Tribute to William Earl, 140
Godwit, Bar-tailed, 13
Hudsonian, 13
Marbled, 13
Golden-Plover, American, 12
Pacific, 12
Goldeneye, Barrow's, 12
Common, 12
Goldenrod, 538
Canada, 300
Northern, 300
Stiff, 260
Goldfinch, American, 179
Gonothyraea loveni, 557
Goodyear, M.A. Extralimital Sighting of a Polar Bear, *Ursus maritimus*, in northeast Saskatchewan, 648
Goose, Canada, 11,227
Emperor, 11
Great White-fronted, 11
Greater Snow, 608
Lesser Snow, 608
Snow, 11,226

Gordia, 578
Goshawk, Northern, 12,479
Gosselin, M., E.L. Bousfield, and S.D. MacDonald. A Tribute to William Earl Godfrey, 1910–2002, 140
Gough, W.A., 523
Goward, T. On the Dispersal of Hair Lichens (*Bryoria*) in High-Elevation Oldgrowth Conifer Forests, 44
Goward, T. On the Vertical Zonation of Hair Lichens (*Bryoria*) in the Canopies of High-elevation Oldgrowth Conifer Forests, 39
Goward, T. and A. Arsenault. Notes on the *Populus* "Drip-zone Effect" on Lichens in Well-ventilated Stands in East-central British Columbia, 61
Grama, Blue, 25,425,645
Sideoats, 218,425
Grammaria abietina, 561
gracilis, 557
Grass, 213
Alpine Holy, 284
Arctic Blue, 452
Buffalo, 645
Creeping Bent, 281
Giant Reed, 103
Hair, 453
Indian, 218
June, 25
Narrow-Leafed Cotton, 213
Nuttall's Alkali, 285
Orchard, 282
Polar Alkali, 285
Red Bent, 281,452
Reed Canary, 103,168,284,452
Spreading Alkali, 285
Western Porcupine, 260
Western Rye, 283
Grass-of-Parnassus, Fringed, 294
Grebe, Horned, 11
Pied-billed, 11
Red-necked, 11
Western, 11
Greenland, Distribution and Conservation of the Harlequin Duck, *Histrionicus histrionicus*, in, 249
Greenling, Painted, 118
Grèf, A., J. Gilhen and J.D. Adams. The Wood Turtle, *Glyptemys insculpta*, at River Denys: A Second Population for Cape Breton Island, Nova Scotia, 415
Grosbeak, Evening, 177
Pine, 16
Ground-cone, 298
Groundhog, 591
Groundsel, Common, 300
Rocky Mountain, 300
Grouse, 365
Blue, 7
Red, 480
Ruffed, 12,177,313,365
Sharp-tailed, 12,227,479
Spruce, 12
Grouseberry, 355
Grove, C., 190
Grus americana, 224
canadensis, 12,224
Grus canadensis, Nesting in the Yorkton Wetland Complex, Saskatchewan, Sandhill Crane, 224
Guillemot, Pigeon, 13,53
Gull, Black-headed, 13
Bonaparte's, 13
Glaucous, 13
Glaucous-winged, 13,604
Great Black-backed, 70
Herring, 13,70
Ivory, 13
Mew, 13
Ring-billed, 13
Ross's, 13
Sabine's, 13
Thayer's, 13
Gulo gulo, 18,357,364,566
Gutierrezia sarothrae, 645
Gymnocarpium dryopteris, 650
dryopteris ssp. *dryopteris*, 279,449
jessoense ssp. *parvulum*, 450
Gyrfalcon, 7,479

Habenaria hyperborea, 454
obtusata, 454
Hackberry, 218
Haedrich, R.L., 440
Haematopus bachmani, 13
Hairgrass, Mountain, 452
Slender, 452
Hake, Silver, 475
Halecium beanii, 558
curvicaule, 561
halecinum, 558
labrosum, 558
lankesteri, 557
muricatum, 557
scutum, 559
sessile, 559
undulatum, 559
Halenia deflexa, 448
Haliaeetus leucocephalus, 12,601
Haliaeetus leucocephalus, Feeding on Spawning Plainfin Midshipman, *Porichthys notatus*, at Crescent Beach, British Columbia, Bald Eagles, 601
Hare, Snowshoe, 17,246,306,314,360,591
Harebell, 260
Harrier, Northern, 12,227,479
Harrier, *Circus cyaneus*, Attacks on Greater Sage-Grouse, *Centrocercus urophasianus*, in Southern Alberta, Northern, 479
Harris, I.W.E., C.F. Drury, R.R. Simard, and T.Q. Zhang. Density and Richness of Benthic Invertebrate Populations in the North Sydenham River of Southwestern Ontario (1996-2000) Compared with Those of the St. Clair River (1990-1995), 267
Harris, S.A. An Occurrence of the Hawkweed-Leaved Saxifrage, *Saxifraga hieraciifolia*, in Southern British Columbia, and its Palaeobotanical Implications, 304
Hartlaubella gelatinosa, 561
Hawk, Eastern Red-tailed, 122
Ferruginous, 479
Harlan's, 122
Krider's, 122
Red-tailed, 7,122,179,479
Rough-legged, 12
Sharp-shinned, 12
Swainson's, 12,479

Hawks in Eastern Kansas, Winter Occurrence of Harlan's, *Buteo jamaicensis harlani*, and Krider's, *B. j. borealis*, 122
Hawk's-beard, Annual, 464
Hawkweed, White, 299
Hawthorn, 311
Haxton, T. Movement of Lake Sturgeon, *Acipenser fulvescens*, in a Natural Reach of the Ottawa River, 541
Heal-all, 297
Heard, D.C. 565
Heather, 354
Pink Mountain, 461
Hebda, A., 475
Hedysarum boreale ssp. *mackenzii*, 279
boreale ssp. *mackenzii* f. *niveum*, 295
Helictotrichon hookeri, 262
Hellebore, White, 288
Helminthoidichnites, 578
Hemidactylium scutatum, 19
Hemlock, 362
Coastal Western, 130
Eastern, 590,622
Interior Western, 130
Mountain, 1,130
Western, 1,215,353,566
Hepatica, Sharp-lobed, 650
Herbertus sp., 214
Heron, Great Blue, 7,603
Heteroscelus incanus, 13
Hickory, 19,622
Bitternut, 218,649
Hieracium albiflorum, 278
aurantiacum, 536
caespitosum, 536
florentinum, 536
pilosella, 536
Hierochloe alpina, 67
alpina ssp. *alpina*, 279
Hirundo rustica, 15
Histrionicus histrionicus, 12,249
Histrionicus histrionicus, in Greenland, Distribution and Conservation of the Harlequin Duck, 249
Hobson, K.A., 347
Holloran, M.J. and S.H. Anderson. Direct Identification of Northern Sage-grouse, *Centrocercus urophasianus*, Nest Predators Using Remote Sensing Cameras, 308
Holt, D.W., M.T. Maples, and C. Savok. Black Color Morph of the Brown Lemming, *Lemmus trimucronatus* = *L. sibiricus*, 466
Hookeria sp., 211
Horehound, Northern Water, 463
Hornwort, 291
Horsetail, 103
Field, 450
Marsh, 450
Variegated, 280,450
Houston, C.S., Reviews by, 326,336,337,338
Huckleberry, Red, 214
Hudson, R.J., 196
Huettmann, F., 53
Huettmann, F., Reviews by, 154,321,325,330,332,334,500, 507,662,664,667
Hulteniella integrifolia, 66
Hulteniella integrifolia (Asteraceae), in Québec, Eco-geographical and Cytological Notes on the Entire-leaved Daisy, 66
Hummingbird, Anna's, 14
Rufous, 7
Hutchinson, R. and H. Goulet, Review by, 487
Hydractinia carica, 561
minuta, 561
polyclina, 557
Hydrallmania falcata, 557
Hydroids (Cnidaria) of Northumberland Strait, Atlantic Canada, with Observations on Their Life Cycles and Distributions, Subtidal, 555
Hylocomium splendens, 210,535
Hypericum perforatum, 536
Hypogymnia austerodes, 62
imshaugii, 62
occidentalis, 62
physodes, 62,535
tubulosa, 62

Iris setosa ssp. *interior*, 279
Iris, Wild, 288
Ironwood, 650
Ixoreus naevius, 15

Jackal, Blackbacked, 424
Jackrabbit, White-tailed, 309
Jacob's-ladder, Northern, 462
Tall, 297
Jaeger, Long-tailed, 13
Parasitic, 7
Pomarine, 13
Jay, Blue, 179,193
Gray, 14
Stellar's, 7
John, R., Reviews by, 151,153,320,335,489,659,663,668
Johnston, V., 302
Joyce, T.L., 57
Juglans nigra, 218
Junco hyemalis, 16,179
Junco, Dark-eyed, 16,179
Juncus spp., 103
balticus ssp. *alaskanus*, 449
balticus var. *littoralis*, 279
filiformis, 449
triglumis ssp. *albescens*, 279
Juniper, Common, 213
Ground, 451
Juniperus communis, 211,449
Jutras, J., 377

Kaiser, G., 53
Kalmia microphylla, 211
polifolia, 279
Kamler, J.F., 472
Kamler, J.F. and P.S. Gipson. Space and Habitat Use by Male and Female Raccoons, *Procyon lotor*, in Kansas, 218
Kamler, J.F. and W.B. Ballard. White Color Phase of the Swift Fox, *Vulpes velox*, 468
Kamler, J.F., K. Keeler, G. Wiens, C. Richardson, and P.S. Gipson. Feral Dogs, *Canis familiaris*, Kill Coyote, *Canis latrans*, 123

Kansas, Space and Habitat Use by Male and Female Raccoons, *Procyon lotor*, in, 218
Kansas, Winter Occurrence of Harlan's, *Buteo jamaicensis harlani*, and Krider's, *B. j. borealis*, Hawks in Eastern, 122
Karagatzides, J.D., 523
Keeler, K., 123
Kennedy, C.E., 278
Keratosum maximum, 557
Kestrel, 424
American, 12
Killdeer, 7,311
Kindbergia sp., 211
Kingbird, Eastern, 14,169
Kingfisher, Belted, 14
Kinglet, Golden-crowned, 7,177
Ruby-crowned, 15
Kinley, T.A., J. Bergenske, J.-A. Davies and D. Quinn. Characteristics of Early-Winter Caribou, *Rangifer tarandus caribou*, Feeding Sites in the Southern Purcell Mountains, British Columbia, 352
Kirstein, F., 531
Kittiwake, Black-legged, 13
Knot, Red, 13
Knotweed, Common, 290
Striate, 290
Kobresia hyperborea, 453
myosuroides, 449
siberica, 449
simpliciuscula, 279
Kobresia, Simple, 288
Koeleria cristata, 262
macrantha, 25
Koenigia islandica, 449
Koenigia, Iceland, 455
Kohn, B.E., 419
Koons, D.N. and J.J. Rotella. Have Lesser Scaup, *Aythya affinis*, Reproductive Rates Declined in Parkland Manitoba?, 582

Labrador, Range Extensions of Logperch, *Percina caprodes*, and Longnose Dace, *Rhinichthys cataractae*, in Newfoundland and, 57
Labrador-tea, 461
Lafoea dumosa, 557
fruticosa, 561
gracillima, 557
Lafoeina tenuis, 557
Lagopus spp., 365
lagopus, 12,480
leucurus, 12
mutus, 12
Lamb, E.G. and W. Megill. The Shoreline Fringe Forest and Adjacent Peatlands of the Southern Central British Columbia Coast, 209
Lamprey, Sea, 59
Lane, R.K. and M. Pearman. Comparison of Spring Return Dates of Mountain Bluebirds, *Sialia currucoides*, and Tree Swallows, *Tachycineta bicolor* with Monthly Air Temperatures, 110
Lanius excubitor, 14
Laomedea neglecta, 559
Lapointe, S., L. Bélanger, J.-F. Giroux, B. Filion. Effects of Plant Cover Improvements for Nesting Ducks on Grassland Songbirds, 167
Lappula occidentalis, 279
Larch, 436
Alpine, 353
Larivière, S., 347
Larivière, S., Review by, 504
Larix laricina, 436,590
lyalli, 353
Lark, Horned, 15,169
Larkspur, Tall, 292
Larus argentatus, 13,70
canus, 13
delawarensis, 13
glaucescens, 13,604
hyperboreus, 13
marinus, 70
philadelphia, 13
ridibundus, 13
thayeri, 13
Lasionycteris noctivigans, 652
Lasiurus borealis, 651
cinereus, 652
Lasiurus borealis, from Cypress Hills Provincial Park, Saskatchewan: A Response to Climate Change?, New Records of the Eastern Red Bat, 651
Lathyrus sativus, 198
Lauff, R., Review by, 488
Laurel, Bog, 213
Western Bog, 214
Leather-leaf, 436,461
Ledum groenlandicum, 211,449
Leech, 380
Leek, Wild, 650
Lein, M.R., 76
Lemming, Brown, 7,466
Northern Bog, 17
Norwegian, 467
Siberian, 17
Lemming, *Lemmus trimucronatus* = *L. sibiricus*, Black Color Morph of the Brown, 466
Lemmus lemmus, 467
sibiricus, 17,466
trimucronatus, 466
Lemmus sibiricus, Black Color Morph of the Brown Lemming, *Lemmus trimucronatus*, 466
Lemmus trimucronatus = *L. sibiricus*, Black Color Morph of the Brown Lemming, 466
Lemons, P.R., W.B. Ballard, R.M. Sullivan, and M.A. Sovada. Den Site Activity Patterns of Adult Male and Female Swift Foxes, *Vulpes velox*, in Northwestern Texas, 424
Leonard, T.D., 477
Leopardbane, Snow, 299
Lepeophtheirus salmonis, 634
Lepeophtheirus salmonis, Infestation on Juvenile Pink Salmon, *Oncorhynchus gorbuscha*, in Nearshore Habitat, First Report of a Sea Louse, 634
Lepidium sativum, 280
Lepidozia reptans, 535
Leptarrhena pyrolifolia, 279
Leptogium saturminum, 62
Lepus americanus, 17,246,306,314,360,591
townsendii, 309
Lesquerella arctica ssp. *arctica*, 279
calderi, 279
Leucanthemum integrifolium, 66

Leuckartiara octona, 561
Leucosticte tephrocotis, 16
Lice, Sea, 636
Lichen, 61
  Hair, 39,44
  Horsehair, 352
Lichens (*Bryoria*) in High-Elevation Oldgrowth Conifer Forests, On the Dispersal of Hair, 44
Lichens (*Bryoria*) in the Canopies of High-elevation Oldgrowth Conifer Forests, On the Vertical Zonation of Hair, 39
Lichens in Well-ventilated Stands in East-central British Columbia, Notes on the *Populus* "Dripzone Effect" on, 61
Lily, Alp, 288
  Glacier, 304
Lily-of-the-valley, False, 214,288
Lim, B.K., Reviews by, 487,672
Limnodromus griseus, 13
  scolopaceus, 13
Limosa fedoa, 13
  haemastica, 13
  lapponica, 13
Linard, C., 605
Linaria vulgaris, 280
Lindgren, C.J. A Brief History of Purple Loosestrife, *Lythrum salicaria*, in Manitoba and its Status in 2001, 100
Lindquist, E.S., C.F. Aquadro, D. McClearn, and K.J. McGowan. Field Identification of the Mice *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* in Central New York, 184
Line, J.M., 448
Lingonberry, 213
Linnaea borealis, 211,352
  borealis var. *americana*, 449
Listera, 210
Liverwort, 214
  Leafy, 214
Lloydia serotina, 279
Lobaria hallii, 64
  pulmonaria, 61,352
Lobarion, 63
Lobelia dortmanna, 449
Lobelia, Water, 463
Locoweed, Blackish, 295
  Yellow, 260
Locust, Honey, 218
Logperch, 57
Logperch, *Percina caprodes*, and Longnose Dace, *Rhinichthys cataractae*, in Newfoundland and Labrador, Range Extensions of, 57
Lomatogonium rotatum ssp. *rotatum*, 449
Longspur, Lapland, 7
  Smith's, 7
Lontra canadensis, 35,380
Loon, Common, 11,254
  Pacific, 11
  Red-throated, 7
  Yellow-billed, 11
Loosestrife, Purple, 100
Loosestrife, *Lythrum salicaria*, in Manitoba and its Status in 2001, A Brief History of Purple, 100
Lophodytes cucullatus, 12
Lota lota, 59
Lotus corniculatus, 278
Lougheed, C., 53
Lougheed, L., 53
Louse, Sea, 634
Louse, *Lepeophtheirus salmonis*, Infestation on Juvenile Pink Salmon, *Oncorhynchus gorbuscha*, in Nearshore Habitat, First Report of a Sea, 634
Lousewort, Woolly, 298,463
Lovegrass, Sand, 645
Loxia curvirostra, 16
  leucoptera, 16
Lumpsucker, 254
Lungwort, 352
  Drummond's, 462
Lutra canadensis, 18,115
Lutra canadensis, in a Highly Urbanized Area, Incidence of Mink, *Mustela vison*, and River Otter, 115
Lycopodium alpinum, 279
  clavatum, 214
  clavatum var. *monostachyon*, 279,449
  complanatum, 279,449
Lycopus americanus, 103
  uniflorus, 449
Lynx canadensis, 360
  canadensis canadensis, 360
  canadensis subsolanus, 360
  (Felis) lynx, 360
  lynx, 18
  rufus, 193,361,472
Lynx, 18
  Canada, 360
  Eurasian, 360
Lynx canadensis, in Canada*, A Review of the Canada Lynx, 360
Lynx, *Lynx canadensis*, in Canada*, A Review of the Canada, 360
Lynx rufus, and Raccoons, *Procyon lotor*, Relative to Home Range Boundaries, Capture Locations of Coyotes, *Canis latrans*, Bobcats, 472
Lysimachia thyrsiflora, 103
Lythrum spp., 106
  salicaria, 100
Lythrum salicaria, in Manitoba and its Status in 2001, A Brief History of Purple Loosestrife, 100

Maass, W., 531
MacDonald, S.D., 140
MacNaughton, R.B. Planispiral Burrows from a Recent Lacustrine Beach, Gander Lake, Newfoundland, 577
MacPherson, A., Review by, 666
Madrepora oculata, 440
Magpie, Black-billed, 15,30,308
Mahoney, S.P., 236
Maianthemum canadense, 535
  dilatatum, 211,280
  racemosum, 650
  trifolium, 449
Malaxis brachypoda, 302
  monophyllos var. *brachypoda*, 302
  monophyllos var. *monophyllos*, 302
Malaxis, One-leaved, 302
Malaxis monophyllos var. *brachypoda*, One-leaved Malaxis, new to the Northwest Territories, Canada, 302
Malaxis, new to the Northwest Territories, Canada, *Malaxis monophyllos* var. *brachypoda*, One-leaved, 302

Mallard, 11,254
Mallotus villosus, 70
Maltais, J., 399
Malus fusca, 213
Manitoba and its Status in 2001, A Brief History of Purple Loosestrife, *Lythrum salicaria*, in, 100
Manitoba, First record of the Deepwater Sculpin, *Myoxocephalus thompsonii*, from George Lake in Whiteshell Provincial Park, 642
Manitoba?, Have Lesser Scaup, *Aythya affinis*, Reproductive Rates Declined in Parkland, 582
Manitoba, Sympatric Presence of Low and High Gillraker Forms of Cisco, *Coregonus artedi*, in Lake Athapapuskow, 49
Maple, 378
  Black, 649
  Red, 185,436,469,532,590,622
  Silver, 470
  Sugar, 389,532,590,622,649
Maples, M.T., 466
Marine Turtle Newsletter, 166,344,513,678
Marmot, Alaskan, 7
  Hoary, 17
Marmota broweri, 17
  caligata, 17
  monax, 17,247,591
Marsh-marigold, 456
  Floating, 456
Marten, 246,591
  American, 18,35,190
Marten, *Martes americana*, Reintroduction in Vermont, Assessing an American, 190
Martes americana, 18,35,190,246,591
  pennanti, 193,591
Martes americana, Reintroduction in Vermont, Assessing an American Marten, 190
Masse, D., 377
Matricaria perforata, 280
Mawhinney, K., 236
Mayweed, Scentless, 299
McCarthy, J., Review by, 502
McClearn, D., 184
McDonald, J.E. Jr. Methods for Capturing Free-Ranging Black Bears, *Ursus americanus*, in Difficult Locations, 621
McFarlane-Tranquilla, L., F. Huettmann, C. Lougheed, L. Lougheed, N. Parker, and G. Kaiser. Sightings of Vagrant Pacific Alcids in Desolation Sound, British Columbia, 53
McGowan, K.J., 184
McManus, R., Jr., 611
McNicholl, M.K., Review by, 505
McPherson, M., 82
Meadow-foxtail, Water, 282
Meadowlark, Eastern, 169,177
  Western, 16
Meadowrue, Alpine, 292
  Few-flowered, 292
Mech, L.D. Incidence of Mink, *Mustela vison*, and River Otter, *Lutra canadensis*, in a Highly Urbanized Area, 115
Medicago sativa ssp. *falcata*, 448
Megill, W., 209
Melandrium taimyrense, 456
Melanelia subaurifera, 62
Melanerpes formicivorus, 311
Melanitta fusca, 12
  nigra, 12
  perspicillata, 12
Meleagris gallopavo, sspp. 609,645
  gallopavo intermedia, 645
Meleagris gallopavo intermedia, interactions, Coyote, *Canis latrans* – Rio Grand Turkey, 645
Meles meles, 243
Melic, False, 285
Melilotus alba, 450
  officinalis, 168
Melospiza lincolnii, 16,169
  melodia, 16,169,179
Mentha arvensis, 103
Menyanthes trifoliata, 279,436,449
Menziesia ferruginea, 214
Mephitis mephitis, 30,227,348,380
Mercenaria mercenaria, 555
Merganser, Common, 12
  Hooded, 7
  Red-breasted, 12
Mergus merganser, 12
  serrator, 12
Merlin, 12
Merluccius bilinearis, 475
Mertensia drummondii, 449
Mice *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* in Central New York, Field Identification of the, 184
Microseris borealis, 214
Microtus spp., 245,348,466
  chrotorrhinus, 246
  longicaudus, 17
  miurus, 17
  oeconomus, 17
  pennsylvanicus, 17,246,466
  xanthognathus, 17
Middleton, J., 393
Midshipman, Plainfin, 601
Midshipman, *Porichthys notatus*, at Crescent Beach, British Columbia, Bald Eagles, *Haliaeetus leucocephalus*, Feeding on Spawning Plainfin, 601
Milk-vetch, Indian, 459
  Bodin's, 295
  Chick-pea, 295
  Pulse, 295
Mimulus guttatus, 279
Mink, 115,227,586,591
  American, 18,35,348
Mink, *Mustela vison*, and River Otter, *Lutra canadensis*, in a Highly Urbanized Area, Incidence of, 115
Mink, *Mustela vison*, Populations under Varying Harvest Regimes, Age Structure Differences in American, 35
Minuartia dawsonensis, 279
  elegans, 279
  obtusiloba, 279
  rossii, 449
  rubella, 449
  yukonensis, 279
Miramichi estuary, 562
Mistletoe, 306
Mitella spp., 352
  diphylla, 650
Mitrewort, 352

Molothrus ater, 16,348
Monkeyflower, Yellow, 298
Monkshood, Mountain, 291
Monobrachium parasiticum, 562
parasitum, 562
Montgomery, K., Review by, 505
Moonwort, 450
Moose, 7,316,357,400,547,591
Alaskan, 7
Morton, A.B. and R. Williams. First Report of a Sea Louse, *Lepeophtheirus salmonis*, Infestation on Juvenile Pink Salmon, *Oncorhynchus gorbuscha*, in Nearshore Habitat, 634
Morus rubra,, 218
Moruzzi, T.L., K.J. Royar, C. Grove, R.T. Brooks, C. Bernier, F.L. Thompson, Jr., R.M. DeGraaf, and T.K. Fuller. Assessing an American Marten, *Martes americana*, Reintroduction in Vermont, 190
Moschatel, 298,463
Moss, 395
Motacilla alba, 15
lugens, 15
Mouse, 365,380
Deer, 7,184,246,390
Field, 245
Meadow Jumping, 17
Northwestern Deer, 7,17
Prairie Deer, 185
White-footed, 184,309
Woodland Jumping, 246
Mugwort, Aleutian, 463
Mulberry, Red, 218
Mulinia lateralis, 555
Murray, L., M.H. Papst, and J.D. Reist. First record of the Deepwater Sculpin, *Myoxocephalus thompsonii*, from George Lake in Whiteshell Provincial Park, Manitoba, 642
Murre, Common, 13
Murrelet, Ancient, 13
Kittlitz's, 13
Marbled, 13,53
Mushroom, 380
Muskrat, 17,115,365,380,590
Mustard, Wormseed, 294
Mustela sp., 247
erminea, 18,193,245
frenata, 193,246,313
nivalis, 18,245
vison, 18,35,115,227,348,586,591
Mustela erminea, in a Forested Landscape, Food Habits of Ermine, 245
Mustela frenata, Hunting Behavior in Central West Virginia, Observations of Long-tailed Weasel, 313
Mustela vison, and River Otter, *Lutra canadensis*, in a Highly Urbanized Area, Incidence of Mink, 115
Mustela vison, Populations under Varying Harvest Regimes, Age Structure Differences in American Mink, 35
Myadestes townsendi, 15
Myotis lucifugus, 17,652
Myoxocephalus quadricornis, 643
thompsonii, 642
Myoxocephalus thompsonii, from George Lake in Whiteshell Provincial Park, Manitoba, First record of the Deepwater Sculpin, 642
Myrica gale, 211
Napaeozapus insignis, 246
National Recovery Strategy for Species at Risk in the Sydenham River: A Ecosystem Approach, 678
Needle-and-Thread, 25,285
Neotoma cinerea, 17
Nephroma resupinatum, 62
New Brunswick, Comparison of the Ground Vegetation in Spruce Plantations and Natural Forest in the Greater Fundy Ecosystem, 531
Newfoundland and Labrador, Range Extensions of Logperch, *Percina caprodes*, and Longnose Dace, *Rhinichthys cataractae*, in, 57
Newfoundland and Mainland Populations of North American Black Bears, *Ursus americanus*, Phenotypic Variation in Skull Size and Shape Between, 236
Newfoundland, First Record of Mink Frog, *Rana septentrionalis*, from Insular, 477
Newfoundland, Planispiral Burrows from a Recent Lacustrine Beach, Gander Lake, 577
Newt, Red-spotted, 19
New York, Field Identification of the Mice *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* in Central, 184
Nighthawk, Common, 7
Nightshade, Enchanter's, 296
Nodobryoria, 39,44
abbreviata, 45
oregana, 39,45
Norment, C.J. Patterns of Nestling Feeding in Harris's Sparrows, *Zonotrichia querula* and White-crowned Sparrows, *Z. leucophrys*, in the Northwest Territories, Canada, 203
North America, Status of the Largest Breeding Concentration of Atlantic Puffins, *Fratercula arctica*, in, 70
North Carolina, Marsh Rice Rat, *Oryzomys palustris*, Predation on Forster's Tern, *Sterna forsteri*, Eggs in Coastal, 654
Northwest Territories and Nunavut, Canada, II, Additions and Range Extensions to the Vascular Plant Flora of the Continental, 448
Northwest Territories, Canada, *Malaxis monophyllos* var. *brachypoda*, One-leaved Malaxis, new to the, 302
Northwest Territories, Canada, Patterns of Nestling Feeding in Harris's Sparrows, *Zonotrichia querula* and White-crowned Sparrows, *Z. leucophrys*, in the, 203
Notophthalmus viridescens, 19
Nova Scotia, The Wood Turtle, *Glyptemys insculpta*, at River Denys: A Second Population for Cape Breton Island, 415
Nowellia curvifolia, 535
Nucifraga columbiana, 15
Numenius phaeopus, 13
tahitiensis, 13
Nunavut, Canada, II, Additions and Range Extensions to the Vascular Plant Flora of the Continental Northwest Territories and, 448
Nutcracker, Clark's, 15
Nuthatch, Red-breasted, 7,177
White-breasted, 177
Nutsedge, Purple, 106
Yellow, 106
Nyctea scandiaca, 14

Oak, 19,394
Bur, 218

Chinkapin, 218
Northern Red, 622
Red, 590
Oak-fern, Nahanni, 451
Obelia geniculata, 559
longissima, 557
Oceanodroma furcata, 11
leucorhoa, 11
Ochotona collaris, 17
Octopus bimaculatus, 117
briareus, 117
cyanea, 117
vulgaris, 117
Octopus, Giant Pacific, 117
Octopus, *Enteroctopus dofleini* (Wülker, 1910), An *in situ* Observation of Webover Hunting by the Giant Pacific, 117
Odocoileus hemionus, 18,309,316,357,657
virginianus, 309,316,357,389,407,567,590
Odocoileus hemionus, in Central Colorado, Aggressive Interactions of Rocky Mountain Elk, *Cervus elaphus nelsoni*, During the Calving Season Toward Mule Deer, 316
Odontoschisma denudatum, 535
Oenanthe oenanthe, 15
Ogden, L.E., Review by, 503
Okello, M.M., 196
Oncorhynchus gorbuscha, 59,634
keta, 638
kisutch, 639
nerka, 603,634
tshawytscha, 639
Oncorhynchus gorbuscha, in Nearshore Habitat, First Report of a Sea Louse, *Lepeophtheirus salmonis*, Infestation on Juvenile Pink Salmon, 634
Ondatra zibethicus, 17,115,365,380,590
Onobrychis viciifolia, 280
Ontario, Canopy Interception of Acid Deposition in Southern, 523
Ontario, Lack of Evidence for Impact of the European White Birch, *Betula pendula*, on the Hydrology of Wainfleet Bog, 393
Ontario, Landscape Influence on *Canis* Morphological and Ecological Variation in a Coyote-Wolf *C. lupus* × *latrans* Hybrid Zone, Southeastern, 589
Ontario (1996-2000) Compared with Those of the St. Clair River (1990-1995), Density and Richness of Benthic Invertebrate Populations in the North Sydenham River of Southwestern, 267
Ontario, Winter Bird Use of Urban and Rural Habitats in, 173
Opercularella lacerata, 558
pumila, 557
Oporornis tolmiei, 15
Orchid, Northern Bog, 454
Northern Green, 454
Oreamnos americanus, 18,565
Oreamnos americanus, in East-central British Columbia, Seasonal Habitat Use and Movements of Mountain Goats, 565
Oregonia gracilis, 117
Oritsland, N.A., 430
Orobanche fasciculata, 279
Orthopyxis integra, 557
Oryctolagus cuniculus, 242
Oryzomys palustris, 654
Oryzomys palustris, Predation on Forster's Tern, *Sterna forsteri*, Eggs in Coastal North Carolina, Marsh Rice Rat, 654
Osmerus mordax, 59
Osmorhiza depauperata, 279,449
Osprey, 12
Ostrea excavata, 440
Ostrya virginiana, 650
Otisorex, 82
Ottawa Field-Naturalists' Club Awards for 2002, The, 679
Ottawa Field-Naturalists' Club 14 January 2003, Minutes of the 124th Annual Business Meeting of The, 514
Otter, 380
River, 18,35,115
Sea, 3
Otter, *Lutra canadensis*, in a Highly Urbanized Area, Incidence of Mink, *Mustela vison*, and River, 115
Otus kennicottii, 14
Ouellet, J.-P., 399,546
Ovalipes ocellatus, 555
Ovis dalli, 18
dalli dalli, 7
Owl, Boreal, 14
Great Gray, 14
Great Horned, 14,227,479
Northern Hawk, 14,306
Saw-whet, 14
Short-eared, 14,466
Snowy, 14
Owl, *Surnia ulula*, Nest on a Man-made Structure in Alaska, A Northern Hawk, 306
Oxalis montana, 535
Oxycoccus microcarpus, 449
oxycoccos, 213
Oxylebius pictus, 118
Oxytropis arctica, 449
Oxytropis campestris, 260
Oxytropis campestris ssp. *roaldii*, 279
Oxytropis deflexa, 67
Oxytropis deflexa ssp. *foliolosa*, 449,460
Oxytropis nigrescens ssp. *nigrescens*, 279
Oxyura jamaicensis, 12
Oystercatcher, Black, 13

Pachistima myrsinites, 352
Pagophila eburnea, 13
Paintbrush, Port Clarence, 298
Pandion haliaetus, 12
Panicum virgatum, 218
Panther, Florida, 113
Papaver keelei, 457
macounii ssp. *discolor*, 449
Papst, M.H., 642
Paraonis fulgens, 578
Parelaphostrongylus tenuis, 407
Parker, N., 53
Parmelia hygrophila, 62
sulcata, 62
Parmeliopsis ambigua, 62
hyperopta, 62
Parnassia fimbriata, 279
kotzebuei, 449
palustris var. *neogaea*, 449
Parus major, 424
Passer domesticus, 177

Passerculus sandwichensis, 16
Passerella iliaca, 16
Peanut, Hog, 650
Pearman, M., 110
Pedicularis flammea, 449
lanata, 279,449
macrodonta, 449
parviflora, 463
Peltigera spp., 352
Penguin, Emperor, 231,430
King, 231
Percina caprodes, 57
Percina caprodes, and Longnose Dace, *Rhinichthys cataractae*, in Newfoundland and Labrador, Range Extensions of Logperch, 57
Pericladium mirabile, 560
Perigonimus sessilis, 561
Perisoreus canadensis, 14
Peromyscus spp., 193,309,348
keeni, 17
leucopus, 184
leucopus noveboracensis, 184
maniculatus, 17,184,246,390
maniculatus bairdii, 184
maniculatus gracilis, 184
maniculatus nubiterrae, 184
Peromyscus leucopus noveboracensis and *P. maniculatus gracilis* in Central New York, Field Identification of the Mice, 184
Peromyscus maniculatus gracilis in Central New York, Field Identification of the Mice *Peromyscus leucopus noveboracensis* and, 184
Perry, R. and T.L. Joyce. Range Extensions of Logperch, *Percina caprodes*, and Longnose Dace, *Rhinichthys cataractae*, in Newfoundland and Labrador, 57
Persicaria vivipara, 67
Petasites frigidus ssp. *palmatus*, 449
palmatus, 464
sagitatus, 449
Peterson, A.P., Review by, 337
Petrochelidon pyrrhonota, 15
Petromyzon marinus, 59
Phalacrocorax auritus, 11
pelagicus, 11
Phalaris arundinacea, 103,168,279,449
Phalarope, Red, 13
Red-necked, 7
Wilson's, 169
Phalaropus fulicarius, 13
lobatus, 13
tricolor, 169
Phasianus colchicus, 479
Pheasant, Ring-necked, 479
Phenacomys ungava, 17
Phillips, G.E., 316
Phleum pratense, 168,198,280,536
Phlox hoodii, 262,279
Phlox, Moss, 297
Phoca groenlandica, 121
hispida, 121,433
Phoebastria nigripes, 11
Phoebe, Eastern, 14
Say's, 14
Phragmites australis, 103
Phryma leptostachya, 650
Phyllodoce coerulea, 449
empetriformis, 354,449
glanduliflora, 354
Phylloscopus borealis, 15
Physcia aipolia, 62
Pica hudsonia, 15
pica, 30
Picea spp., 61,203,306,362,394
engelmannii, 40,44,353
engelmannii x *glauca*, 61
glauca, 1,76,130,307,353,378,532,590
glauca X *engelmannii*, 566
mariana, 1,72,130,362,436,532,590
rubens, 532
sitchensis, 1,212
Picoides arcticus, 14
pubescens, 14,179
tridactylus, 14
villosus, 14,177
Pigeon, Band-tailed, 14
Pigmyweed, 458
Pika, Collared, 7
Pike, Northern, 59
Pin-Cherry, 538
Pine, 19,362,394
Eastern White, 590,622
Jack, 91,130
Limber, 91
Lodgepole, 76,91,281,353,362,566
Ponderosa, 91,628
Red, 590
Shore, 213
Whitebark, 353,566
Pinicola enucleator, 16
Pintail, Northern, 12,605
Pintails, *Anas acuta*, Initiate Rapid Follicular Growth During Spring Migration?, Do Female Northern, 605
Pinus spp., 19,362,394
albicaulis, 353,566
banksiana, 91,130
contorta, 61,76,91,211,353,362,566
contorta ssp. *latifolia*, 279
flexilis, 91
ponderosa, 91,628
resinosa, 590
strobus, 590
Pipit, American, 15
Piranga ludoviciana, 16
Placobdella sp., 380
Plagiothecium sp., 211
Plangtichnus, 578
Planolites, 578
Plantago major, 280
Plantain, Common, 298
Platanthera aquilonis, 449
hyperborea, 454
obtusata, 449
Platanus occidentalis, 646
Platismatia glauca, 62
Plectrophenax nivalis, 16,177
Plethodon cinereus, 22
glutinosus, 19
hoffmani, 19
Pleurozium schreberi, 535
Plover, Black-bellied, 12

Semipalmated, 12
Pluvialis dominica, 12
fulva, 12
squatarola, 12
Poa arctica, 67,449
compressa, 280,536
leptocoma, 279
porsildii, 279
pratense, 536
pratensis, 168,196,258
pratensis ssp. *alpigena*, 279
secunda ssp. *secunda*, 279
trivialis, 280
Podiceps auritus, 11
grisegena, 11
Podilymbus podiceps, 11
Poecile atricapillus, 15,179
cincta, 15
gambeli, 15,76
hudsonica, 15
rufescens, 15
Poecile gambeli, to Playback of Different Song Types, Response of Male Mountain Chickadees, 76
Point Pelee Natural History News, 167,343,513,677
Polargrass, 452
Polemonium acutiflorum, 279
boreale, 449
boreale forma *albiflorum*, 448
Polygonum spp., 103
achoreum, 280
aviculare, 280
caurianum ssp. *hudsonianum*, 455
fowleri, 448
hudsonianum, 449
hydropiper, 536
ramosissimum, 448
Polytrichastrum alpinum, 66
Polytrichum spp., 536
commune, 535
formosum, 537
piliferum, 66
strictum, 395
Pondweed, Fine-leaved, 281
Giant, 281,451
Ponomarenko, S., 125
Poole, K.G. A Review of the Canada Lynx, *Lynx canadensis*, in Canada*, 360
Poole, K.G. and D.C. Heard. Seasonal Habitat Use and Movements of Mountain Goats, *Oreamnos americanus*, in East-central British Columbia, 565
Poplar, Balsam, 196
Populus, 61
alba, 536
balsamifera, 196,582
deltoides, 645
grandidentata, 436
tremuloides, 61,76,91,196,362,378,395,436,582,590,652
trichocarpa, 61
Populus "Dripzone Effect" on Lichens in Well-ventilated Stands in East-central British Columbia, Notes on the, 61
Porcupine, 469
American, 17
Porcupine, *Erethizon dorsatum*, Dens in Wisconsin, Death of Gray Wolves, *Canis lupus*, in, 469
Porichthys notatus, 601
Porichthys notatus, at Crescent Beach, British Columbia, Bald Eagles, *Haliaeetus leucocephalus*, Feeding on Spawning Plainfin Midshipman, 601
Porzana carolina, 12
Potamogeton spp., 273
filiformis var. *borealis*, 279
natans, 449
obtusifolius, 449
porsildiorum, 451
richardsonii, 449
vaginatus, 279,449
Potentilla anserina, 103
arguta, 260
hyparctica, 449
nivea, 279,449
porsildiorum, 449
recta, 536
tridentata, 449
Powell, K.G., 477
Primrose, Greenland, 296
Mealy, 462
Primula egaliksensis, 279
incana, 449
Procyon lotor, 30,193,218,227,348,380,472,591
Procyon lotor, in Kansas, Space and Habitat Use by Male and Female Raccoons, 218
Procyon lotor, Relative to Home Range Boundaries, Capture Locations of Coyotes, *Canis latrans*, Bobcats, *Lynx rufus*, and Raccoons, 472
Pronghorn, 309
Prosopium cylindraceum, 59
Prunella vulgaris ssp. *lanceolata*, 278
Prunus pensylvanica, 538
serotina, 19,395
virginiana, 417
Psathyrostachys juncea, 283
Pseudacris triseriata, 477
Pseudevernion, 63
Pseudocyphellaria anomala, 61
Pseudotriton ruber, 19
Pseudotsuga menziesii, 45,61,91,353,362,628
Ptarmigan, 365
Rock, 12
White-tailed, 12
Willow, 12
Pteridium aquilinum, 214
Ptilidium ciliare, 66
Ptychoramphus aleuticus, 13
Puccinellia deschampsioides, 279
distans, 280
nuttalliana, 280
Puffin, Atlantic, 70
Horned, 14
Tufted, 14
Puffins, *Fratercula arctica*, in North America, Status of the Largest Breeding Concentration of Atlantic, 70
Puffinus carneipes, 11
griseus, 11
tenuirostris, 11
Puma concolor, 566
concolor coryi, 113
Pungitius pungitius, 59
Purshia tridentata, 628
Pyrola minor, 280,449

Quail, Japanese, 348
Québec, Eco-geographical and Cytological Notes on the Entire-leaved Daisy, *Hulteniella integrifolia* (Asteraceae), in, 66
Québec, Ecological Aspects of a Wood Turtle, *Glyptemys insculpta*, Population at the Northern Limit of its Range in, 377
Quebec, Historical Changes and Current Distribution of Caribou, *Rangifer tarandus*, in, 399
Quercus spp., 19,394
macrocarpa, 218
muhlenbergii, 218
rubra, 590,622
Quinn, D., 352

Rabbit, European, 242
Rabbitbrush, 645
Raccoon, 30,193,218,227,348,380,472,591
Raccoons, *Procyon lotor*, in Kansas, Space and Habitat Use by Male and Female, 218
Raccoons, *Procyon lotor*, Relative to Home Range Boundaries, Capture Locations of Coyotes, *Canis latrans*, Bobcats, *Lynx rufus*, and, 472
Racomitrium sp., 213
Ragweed, Mount Sheldon, 299
Western, 645
Ragwort, Tundra, 300
Ramalina thrausta, 62
Rana clamitans, 477
pipiens, 477
septentrionalis, 477
sylvatica, 477
Rana septentrionalis, from Insular Newfoundland, First Record of Mink Frog, 477
Rangifer tarandus, 18,120,253,399
tarandus caribou, 7,39,44,352,546
tarandus granti, 7
tarandus platyrhynchus, 433
Rangifer tarandus caribou, An Aerial Survey Technique for the Forest-Dwelling Ecotype of Woodland Caribou, 546
Rangifer tarandus caribou, Feeding Sites in the Southern Purcell Mountains, British Columbia, Characteristics of Early-Winter Caribou, 352
Rangifer tarandus, in Quebec, Historical Changes and Current Distribution of Caribou, 399
Ranunculus acris, 536
aquatilis var. *eradicatus*, 280
aquatilis var. *hispidulus*, 450
eschscholtzii, 280
flammula, 280,449
flammula var. *filiformis*, 449
nivalis, 449
pallasii, 449
pedatifidus ssp. *affinis*, 280
pygmaeus, 449
sulphureus, 449
trichophyllus var. *hipidulus*, 456
Raspberry, 538
Creeping, 295
Dwarf, 295
Rat, Marsh Rice, 654
Rat, *Oryzomys palustris*, Predation on Forster's Tern, *Sterna forsteri*, Eggs in Coastal North Carolina, Marsh Rice, 654
Rattlesnake, Massasauga, 393
Raven, Common, 15,30,227,308
Reading, K.L., 448
Reakoff, J.L., 306
Reakoff, M.L., J.L. Reakoff and T. Craig. A Northern Hawk Owl, *Surnia ulula*, Nest on a Man-made Structure in Alaska, 306
Recovery: An Endangered Species Newsletter, 166,344,678
Recovery Strategy for Bowhead Whales in Canadian Eastern Arctic, 678
Redcedar, Western, 353,566
Redhead, 7
Redpoll, 611
Common, 7
Hoary, 16
Redpoll, *Carduelis* sp., Winter Visitations in Atlantic Canada, Supposed Periodicity of, 611
Redstart, American, 7,206
Redtop, 168
Spike, 281
Reedgrass, Northern, 282
Purple, 282
Reeves, H.M., Review by, 661
Regehr, H.M., 70
Regulus calendula, 15
satrapa, 15,177
Reindeer, Svalbard, 433
Reist, J.D., 642
Rhinichthys cataractae, 57
Rhinichthys cataractae, in Newfoundland and Labrador, Range Extensions of Logperch, *Percina caprodes*, and Longnose Dace, 57
Rhizocaulus verticillatus, 557
Rhizomnium sp., 214
Rhodostethia rosea, 13
Rhytidiadelphus sp., 211
Richardson, C., 123
Riparia riparia, 15
Ripley, E.A., 257
Rissa tridactyla, 13
Rithropanopeus harrisii, 555
Robards, M.D., 119
Robichaud, J., 82
Robin, American, 15,177,311
Robin, *Turdus migratorius*, Autumn and Winter Breeding Records for the American, 311
Rockcress, Boivin's, 292
Cody's, 292
Holboell's, 292
Lyre-leaved, 292
Rockfish, Copper, 118
Puget Sound, 118
Rodway, M.S., H.M. Regehr, and J.W. Chardine. Status of the Largest Breeding Concentration of Atlantic Puffins, *Fratercula arctica*, in North America, 70
Romo, J.T. Reintroducing Fire for Conservation of Fescue Prairie Association Remnants in the Northern Great Plains, 89
Rosa spp., 258
woodsii, 280
Rose, 258
Western, 295
Rosemary, Bog, 296
Rosy-Finch, Gray-crowned, 16
Rotella, J.J., 582

Royar, K.J., 190
Rubus spp., 72,533,594
acaulus, 459
arcticus ssp. *acaulis*, 449
pedatus, 211,280
pubescens, 280
strigosus, 535
Rumex acetosa ssp. *alpestris*, 280
acetosella, 536
crispus, 536
occidentalis, 103
Rush, Baltic, 288
Dwarf Scouring, 450
Spike, 103
Whitish, 288
Rye, Canada Wild, 452
Russian Wild, 283
Thick-spike Wild, 283

Sage, 25
Prairie, 258
Silver, 25
Sage-Grouse, Greater, 25,479
Northern, 308
Sage-Grouse, *Centrocercus urophasianus*, in Canada, Distribution, Abundance, and Status of the Greater, 25
Sage-Grouse, *Centrocercus urophasianus*, in Southern Alberta, Northern Harrier, *Circus cyaneus*, Attacks on Greater, 479
Sage-grouse, *Centrocercus urophasianus*, Nest Predators Using Remote Sensing Cameras, Direct Identification of Northern, 308
Sagebrush, 25,645
Sagittaria spp., 168
Saher, D.J., 479
Salal, 213
Salamander, Four-toed, 19
Jefferson, 19
Mountain Dusky, 19
Northern Red, 19
Redback, 19
Ridge, 19
Slimy, 19
Valley, 19
Woodland, 19
Salamanders Along Forest-Farmland Edges, Distribution of, and Microhabitat Use by, Woodland, 19
Salix spp., 103,203
alaxensis ssp. *longistylis*, 280
arbusculoides, 280
arctica, 66,280
arctophila, 280
athabascensis, 449
brachycarpa ssp. *niphoclada*, 289
commutata, 280
fuscescens, 280
hastata, 280
herbacea, 67
lanata ssp. *richardsonii*, 289
lutea, 449
monticola, 289
niphoclada, 280
polaris, 280,449
polaris ssp. *pseudopolaris*, 454
pseudomonticola, 280
reticulata, 67
richardsonii, 280
rotundifolia ssp. *rotundifolia*, 280,448
Salmo salar, 59,634
trutta, 634
Salmon, Atlantic, 59,634
Kokanee, 603
Pink, 59,634
Sockeye, 634
Salmon, *Oncorhynchus gorbuscha*, in Nearshore Habitat, First Report of a Sea Louse, *Lepeophtheirus salmonis*, Infestation on Juvenile Pink, 634
Salvelinus alpinus, 59,254,634
fontinalis, 59
namaycush, 59,642
Sambucus racemosa, 538
Sander vitreus, 542
Sander-Regier, R., Reviews by, 157,158,159,327,339,497,498
Sanderling, 13
Sandpiper, Baird's, 13
Buff-breasted, 13
Least, 7
Pectoral, 13
Rock, 13
Semipalmated, 13
Solitary, 13
Spotted, 13
Upland, 13
Western, 13
Sandreed, Prairie, 645
Sandwort, Alpine, 291
Boreal, 456
Northern, 290
Rock, 290
Sanguisorba canadensis ssp. *latifolia*, 280
officinalis, 213
Sapsucker, Red-breasted, 7
Yellow-bellied, 7
Sarsia tubulosa, 561
Saskatchewan: A Response to Climate Change?, New Records of the Eastern Red Bat, *Lasiurus borealis*, from Cypress Hills Provincial Park, 651
Saskatchewan, Effects of Season of Burning on the Microenvironment of Fescue Prairie in Central, 257
Saskatchewan, Extralimital Sighting of a Polar Bear, *Ursus maritimus*, in northeast, 648
Saskatchewan, Sandhill Crane, *Grus canadensis*, Nesting in the Yorkton Wetland Complex, 224
Savok, C., 466
Saxifraga aizoides, 67
caespitosa ssp. *uniflora*, 449
cernua, 449
foliolosa, 449
hieracifolia, 304,449
hirculus, 449
nelsoniana ssp. *porsildiana*, 449
nivalis, 449
oppositifolia, 67
punctata ssp. *porsildiana*, 459
Saxifraga hieraciifolia, in Southern British Columbia, and its Palaeobotanical Implications, An Occurrence of the Hawkweed-Leaved Saxifrage, 304
Saxifrage, Alpine, 459
Hawkweed-Leaved, 304
Leather-leaved, 294

Nodding, 458
Northern Golden, 458
Tufted, 458
Yellow Marsh, 459
Saxifrage, *Saxifraga hieraciifolia*, in Southern British Columbia, and its Palaeobotanical Implications, An Occurrence of the Hawkweed-Leaved, 304
Sayornis phoebe, 14
saya, 14
Scaup, Greater, 12,582
Lesser, 12,582
Scaup, *Aythya affinis*, Reproductive Rates Declined in Parkland Manitoba?, Have Lesser, 582
Schizachne purpurascens, 280
Schultz, R.N., 469
Scirpus spp., 103
acutus, 226
caespitosus ssp. *austriacus*, 280
validus, 449
Scizachyrium scoparium, 218
Scolochloa festucacea, 103
Scoter, Black, 12
Surf, 12
White-winged, 12
Scotter, G.W., Review by, 159
Screech-Owl, Western, 14
Scrub-Jay, Western, 311
Sculpin, Deepwater, 642
Fourhorn, 643
Mottled, 59
Slimy, 59
Sculpin, *Myoxocephalus thompsonii*, from George Lake in Whiteshell Provincial Park, Manitoba, First record of the Deepwater, 642
Scyliorhinus retifer, 475
retifer retifer, 476
Scyliorhinus retifer (Garman, 1881), New to the Canadian Atlantic Ichthyofauna, The Chain Dogfish, 475
Sea-blite, 456
Seal, 121
Ringed, 433
Sears, H.J., J.B. Theberge, M.T. Theberge, I. Thornton, and G.D. Campbell. Landscape Influence on *Canis* Morphological and Ecological Variation in a Coyote-Wolf *C. lupus* × *latrans* Hybrid Zone, Southeastern Ontario, 589
Sebastes caurinus, 118
emphaeus, 118
Seburn, D., Reviews by, 327,332
Seburn, D.C. Population Structure, Growth, and Age Estimation of Spotted Turtles, *Clemmys guttata*, Near their Northern Limit: an 18-Year Follow-up, 436
Sedge, 103,258
Alpine, 287
Awned, 285
Bent, 286
Blunt, 287
Bog, 287
Bristle, 287
Broad-wing, 453
Broad-leaved, 650
Brownish, 286
Buxbaum's, 286
Dark-brown, 286
Dunhead, 287
Few-flowered, 214
Few-seeded Bog, 287
Franklin's, 286
Garber's, 286
Glacier, 287
Goosegrass, 286
Green, 287
Hairlike, 286
Long-stalked, 650
Low Northern, 286
Northern Clustered, 285,452
Plantain-leaved, 650
Thick-headed, 287
Threadleaf, 197
Two-coloured, 286
William's, 287
Yellow, 286
Yukon, 286
Seiurus noveboracensis, 15
Selaginopsis alternitheca, 562
Selasphorus rufus, 14
Semotilus margarita, 59
Senecio indecorus, 280
jacobaea, 536
sheldonensis, 280
streptanthifolius, 280
tundricola, 280
vulgaris, 280
Sertularella polyzonias, 557
rugosa, 560
tenella, 561
Sertularia argentea, 561
cupressina, 560
fabricii, 560
latiuscula, 557
pumila, 561
similis, 560
Setophaga ruticilla, 15,206
Shad, American, 59
Shearwater, Flesh-footed, 11
Short-tailed, 11
Sooty, 11
Sheep, Dall, 7
Domestic, 309
Shepherdia canadensis, 449
Shooting Star, Few Flowered, 304
Shoveler, Northern, 12
Shrew, American Water, 7
Arctic, 83
Cinereus, 17
Dusky, 17,82
Masked, 17,87,246
Montane, 17
North American Pygmy, 82
Pygmy, 17,82
Short-tailed, 246,390
Tiny, 7
Tundra, 7
Vagrant, 82
Water, 82
Shrews (*Sorex*)? Revisiting the Question Using DNA Sequence Data, Are There Two Species of Pygmy, 82
Shrike, Northern, 7
Sialia currucoides, 15,110

Sialia currucoides, and Tree Swallows, *Tachycineta bicolor* with Monthly Air Temperatures, Comparison of Spring Return Dates of Mountain Bluebirds, 110
Sibbaldia procumbens, 280
Sibbaldia, 295
Silene acaulis, 67
acaulis ssp. *acaulis*, 280
cucubalis, 260
involucrata ssp. *involucrata*, 280
taimyrensis, 280,449
uralensis ssp. *ogilviensis*, 448
Simard, R.R., 267
Siskin, Pine, 16,177
Sistrurus catenatus catenatus, 393
Sitta canadensis, 15,177
carolinensis, 177
Skua, South Polar, 13
Skunk, Striped, 30,227,348,380
Smartweed, 103
Smelt, Rainbow, 59
Smilacina trifolia, 454
Smith, B.W., C.A. Dobony, J.W. Edwards, and W.M. Ford. Observations of Long-tailed Weasel, *Mustela frenata*, Hunting Behavior in Central West Virginia, 313
Smith, C.M., Review by, 675
Smith, P.G.R. Winter Bird Use of Urban and Rural Habitats in Ontario, 173
Smith, T., Reviews by, 506,672
Snag, 215
Snakeroot, White, 650
Snakeweed, 645
Snipe, Common, 13,169
Snowberry, Western, 258
Soapberry, 460
Solidago canadensis var. *salebrosa*, 280
graminifolia, 535
missouriensis, 262
multiradiata, 280
rigida, 260
rugosa, 537
Solitaire, Townsend's, 15
Solomon's Seal, False, 650
Somateria mollissima, 12,230,608
spectabilis, 12
Somateria mollissima, Physical Condition of an Animal, Using as an Example the Common Eider, 230
Sonchus asper, 280
Sora, 7
Sorex spp., 82,246
araneus, 85
arcticus, 83
asper, 85
caecutiens, 85
cinereus, 17,84,246
fumeus, 85
granarius, 85
haydeni, 84
hoyi, 17,82
hoyi eximius, 82
hoyi hoyi, 82
hoyi montanus, 82
hoyi thompsoni, 82
hoyi winnemana, 82
maritimensis, 83
monticolus, 17,82
pacificus, 84
palustris, 17,82
shinto, 85
thompsoni, 82
trowbridgii, 84
tundrensis, 17,85
vagrans, 82
yukonicus, 17
(*Sorex*)? Revisiting the Question Using DNA Sequence Data, Are There Two Species of Pygmy Shrews, 82
Sorghastrum nutans, 218
Sorrel, Green, 290
Sovada, M.A., 424
Sow-thistle, Spiny, 300
Sparganium eurycarpum, 168
minimum, 280
Sparrow, American Tree, 16,179
Brewer's, 7
Chipping, 7,169
Clay-colored, 16
Fox, 16
Gambel's White-crowned, 203
Golden-crowned, 16,206
Harris's, 203
House, 177
Lark, 16
Lincoln's, 16,169
Nelson's Sharp-tailed, 169
Rufous-collared, 206
Savannah, 16,169
Seaside, 654
Song, 7,169,179
Swamp, 169
White-crowned, 16,203,617
White-throated, 16,206
Sparrows, *Z. leucophrys*, in the Northwest Territories, Canada, Patterns of Nestling Feeding in Harris's Sparrows, *Zonotrichia querula* and White-crowned, 203
Sparrows, *Zonotrichia querula* and White-crowned Sparrows, *Z. leucophrys*, in the Northwest Territories, Canada, Patterns of Nestling Feeding in Harris's, 203
Spartina alterniflora, 654
Spears, B.L., W.B. Ballard, M.C. Wallace, R.D. Applegate, and P.S. Gipson. Coyote, *Canis latrans* – Rio Grand Turkey, *Meleagris gallopavo intermedia*, interactions, 645
Spearwort, Creeping, 292,457
Spergularia rubra, 280
Spermophilus spp., 347,365
parryii, 17
richardsonii, 30,308
tricemlineatus, 308
Sphagnum spp., 211,393,436
girgensohnii, 535
Sphagnum, 436
Sphyrapicus ruber, 14
varius, 14
Spiraea, 459
Spiraea beauverdiana, 449
Spirodesmos archimedeus, 577
interruptus, 578
Spizella arborea, 16,179
breweri, 16
pallida, 16
passerina, 16,169

Spleenwort, Narrow-leaved, 650
Sporobolus cryptandrus, 425,645
Spruce, 203,306,362,394,566
Black, 1,72,130,362,436,532,590
Engelmann, 40,44,353
Red, 532
Sitka, 1,215
Sub-Boreal, 130
White, 1,76,130,307,353,378,532,590
Spurry, Purple Sand, 291
Squirrel, American Red, 17
Arctic Ground, 7
Flying, 193,365
Ground, 347,365
Northern Flying, 17
Red, 193,246,365
Richardson's Ground, 30,308
Thirteen-lined Ground, 308
Staniforth, J., 278
Starflower, Northern, 213
Starling, European, 15,177
Starwort, Boreal, 291
Thick-leaved, 456
Stelgidopteryx serripennis, 15
Stellaria borealis, 280,449
calycantha, 456
crassifolia, 449
graminifolia, 536
longifolia, 280
media, 280
Stephens, R.M., A.W. Alldredge, and G.E. Phillips. Aggressive Interactions of Rocky Mountain Elk, *Cervus elaphus nelsoni*, During the Calving Season Toward Mule Deer, *Odocoileus hemionus*, in Central Colorado, 316
Stercorarius longicaudus, 13
maccormicki, 13
parasiticus, 13
pomarinus, 13
Sterna aleutica, 13
caspia, 13
forsteri, 654
hirundo, 13
paradisaea, 13,309
Sterna forsteri, Eggs in Coastal North Carolina, Marsh Rice Rat, *Oryzomys palustris*, Predation on Forster's Tern, 654
Stewart, D.T., M. McPherson, J. Robichaud and L. Fumagalli. Are There Two Species of Pygmy Shrews (*Sorex*)? Revisiting the Question Using DNA Sequence Data, 82
Stichwort, Ross', 456
Stickleback, Ninespine, 59
Threespine, 59
Stickseed, Western, 297
Sticta fuliginosa, 61
Stint, Red-necked, 13
Stipa comata, 25,280
spartea, 262
spartea var. *curtiseta*, 260
viridula, 262
Stitchwort, Yukon, 291
Storm-Petrel, Fork-tailed, 11
Leach's, 11
Strawberry, 380
Wild, 294
Streptopus amplexifolius ssp. *americanus*, 280
Strix nebulosa, 14
Struik, C.L., 601
Stubblefield, W.A., 119
Sturgeon, Atlantic, 59
Lake, 541
Sturgeon, *Acipenser fulvescens*, in a Natural Reach of the Ottawa River, Movement of Lake, 541
Sturnella magna, 169,177
neglecta, 16
Sturnus vulgaris, 15,177
Suaeda calceoliformis, 449
Subularia aquatica ssp. *americana*, 280,449
Sucker, Longnose, 59
White, 59
Sullivan, R.M., 424
Sundew, Round-Leafed, 213
Surfbird, 7
Surnia ulula, 14,306
Surnia ulula, Nest on a Man-made Structure in Alaska, A Northern Hawk Owl, 306
Swallow, Bank, 15
Barn, 7
Cliff, 15
Northern Rough-winged, 15
Tree, 15,110
Violet-green, 15
Swallows, *Tachycineta bicolor* with Monthly Air Temperatures, Comparison of Spring Return Dates of Mountain Bluebirds, *Sialia currucoides*, and Tree, 110
Swan, Trumpeter, 11
Tundra, 11
Sweet-cicely, Blunt-fruited, 296
Sweet-Clover, Yellow, 168
Sweet-vetch, Boreal, 295
Swift, Vaux's, 14
Switchgrass, 218
Sycamore, 646
Sylvilagus sp., 314
floridanus, 591
Symphoricarpos occidentalis, 258
Symplectoscyphus tricuspidatus, 557
Synaptomys borealis, 6
cooperi, 247
Syncoryne mirabilis, 561
Synthliboramphus antiquus, 13

Tachycineta bicolor, 15,110
thalassina, 15
Tachycineta bicolor with Monthly Air Temperatures, Comparison of Spring Return Dates of Mountain Bluebirds, *Sialia currucoides*, and Tree Swallows, 110
Tamarack, 590
Tamarisk, 645
Tamarix chinensis, 645
Tamias minimus, 17
striatus, 246,591
Tamiasciurus hudsonicus, 17,193,246,365
Tanacetum vulgare, 536
Tanager, Western, 7
Tanseymustard, Northern, 293
Taraxacum lyratum, 280,449
officinale, 197
phymatocarpum, 464

Tarragon, 299
Tattler, Wandering, 13
Taxidea taxus, 308,348
Taxus brevifolia, 213
canadensis, 389
Taxus canadensis, Small Mammal Abundance and Diversity in Forests with and without Canada Yew, 389
Tea, Labrador, 213
Teal, Blue-winged, 12,227,314
Cinnamon, 12
Green-winged, 12
Tern, Aleutian, 7
Arctic, 13,309
Black, 13
Caspian, 13
Common, 13
Forster's, 654
Tern, *Sterna forsteri*, Eggs in Coastal North Carolina, Marsh Rice Rat, *Oryzomys palustris*, Predation on Forster's, 654
Texas, Den Site Activity Patterns of Adult Male and Female Swift Foxes, *Vulpes velox*, in Northwestern, 424
Thalictrum alpinum, 280
sparsiflorum ssp. *richardsonii*, 280
Thallose, 214
Theberge, J.B., 589
Theberge, M.T., 589
Thistle, 103
Thompson, F.L. Jr., 190
Thompson, I.D., Review by 155
Thornton, I., 589
Thrush, Gray-cheeked, 15
Hermit, 15
Swainson's, 15
Varied, 15
Thuiaria alternitheca, 562
argentea, 561
articulata, 562
carica, 562
kolaensis, 562
laxa, 560
thuiarioides, 561
Thuja occidentalis, 470,590
plicata, 61,212,353,566
Tiarella spp., 352
Tilia americana, 590,650
Tillaea aquatica, 458
Timothy, 168,285
Titman, R.D., 377
Tits, Great, 424
Toad, 380
American, 477
Tofieldia glutinosa, 213
pusilla, 67
Tokaryk, T.T., Reviews by, 340,341
Trefoil, Birds-foot, 295
Trichophorum caespitosum, 211
Trientalis arctica, 213
Trifolium spp., 168
pratense, 280
repens, 197
Tringa flavipes, 13
melanoleuca, 13
solitaria, 13
Troglodytes troglodytes, 15
Trout, Brook, 59
Lake, 59,642
Sea, 634
Tryngites subruficollis, 13
Tsuga spp., 362
canadensis, 590,622
heterophylla, 1,212,353,566
mertensiana, 1
Tsuji, L.J.S., 523
Tubularia crocea, 561
indivisa, 561
Tuckermannopsis chlorophylla, 62
ciliaris, 64
Turdus migratorius, 15,177,311
Turdus migratorius, Autumn and Winter Breeding Records for the American Robin, 311
Turkey, Eastern Wild, 609
Rio Grand, 645
Wild, 645
Turkey, *Meleagris gallopavo intermedia*, interactions, Coyote, *Canis latrans* – Rio Grand, 645
Turnstone, Black, 13
Ruddy, 13
Turtle, Blanding's, 415
Bog, 415
Eastern Painted, 415
Snapping, 415
Spotted, 415,436
Western Pond, 415
Wood, 377,415
Turtle, *Glyptemys insculpta*, at River Denys: A Second Population for Cape Breton Island, Nova Scotia, The Wood, 415
Turtle, *Glyptemys insculpta*, Population at the Northern Limit of its Range in Québec, Ecological Aspects of a Wood, 377
Turtles, *Clemmys guttata*, Near their Northern Limit: an 18-Year Follow-up, Population Structure, Growth, and Age Estimation of Spotted, 436
Twinflower, 214,352,463
Twistedstalk, Clasping, 288
Tympanuchus phasianellus, 12,227,479
Typha angustifolia, 101,168
latifolia, 103
x *glauca*, 103
Tyrannus forficatus, 14
tyrannus, 14,169

Ulmus americana, 218,590
Uria aalge, 13
Urocyon cinereoargenteus, 468
Urosalpinx cinerea, 555
Ursus americanus, 18,113,193,236,407,566,591,621,626
americanus floridanus, 113
americanus hamiltoni, 236
americanus luteolus, 113
arctos, 18,566
horribilis, 30
maritimus, 120,433,648
Ursus americanus, Associated with Elevated Train Trestles, Mortality of Black Bears, 113
Ursus americanus, Denning Chronology and Den Site Selection in the Northeastern Cascades of Washington, Black Bear, 626

Ursus americanus, in Difficult Locations, Methods for Capturing Free-Ranging Black Bears, 621
Ursus maritimus, in northeast Saskatchewan, Extralimital Sighting of a Polar Bear, 648
Ursus americanus, Phenotypic Variation in Skull Size and Shape Between Newfoundland and Mainland Populations of North American Black Bears, 236
Usnea lapponica, 62
Utricularia minor, 280
Uvularia grandiflora, 650

Vaccinium spp., 213,352,594
corymbosum, 395
macrocarpon, 436
myrtilloides, 535
ovalifolium, 448
oxycoccus, 436
parvifolium, 212
uliginosum, 213
vitis-idaea, 213
Vahlodea atropurpurea ssp. *latifolia*, 449
Van Why, K.R. and M.J. Chamberlain. Mortality of Black Bears, *Ursus americanus*, Associated with Elevated Train Trestles, 113
Veinotte, C., B. Freedman, W. Maass, and F. Kirstein. Comparison of the Ground Vegetation in Spruce Plantations and Natural Forest in the Greater Fundy Ecosystem, New Brunswick, 531
Veratrum viride ssp. *eschscholtzii*, 280
Verbena hastata, 278
Vermivora celata, 15
peregrina, 15
Vermont, Assessing an American Marten, *Martes americana*, Reintroduction in, 190
Vervain, Blue, 297
Vetch, American, 260
Tufted, 168
Viburnum alnifolium, 535
Vicia americana, 103,260
cracca, 168
Viola adunca, 262,449
epipsila ssp. *repens*, 280,449
langsdorfii, 280
nephrophylla, 280
renifolia var. *brainerdii*, 449
Violet, Alaska, 296
Dwarf Marsh, 296,460
Hook-spur, 460
Kidney-leaved, 460
Northern Bog, 296
Vireo gilvus, 14
solitarius, 14
Vireo, Blue-headed, 14
Warbling, 14
Virginia, Observations of Long-tailed Weasel, *Mustela frenata*, Hunting Behavior in Central West, 313
Virgl, J.A., S.P. Mahoney, and K. Mawhinney. Phenotypic Variation in Skull Size and Shape Between Newfoundland and Mainland Populations of North American Black Bears, *Ursus americanus*, 236
Vole, 245,365
Chestnut-cheeked, 17
Eastern Heather, 7
Insular, 17
Long-tailed, 7
Meadow, 17,246,466
Northern, 17
Northern Red-backed, 7
Red-Backed, 246
Singing, 7
Southern Red-backed, 390
Taiga, 7
Tundra, 7
Yellow-Nosed, 246
Vulpes fulva, 380
macrotis, 123,424,468
velox, 30,123,424,468
vulpes, 17,30,123,227,308,348,365,424,468,472,586,591
Vulpes velox, in Northwestern Texas, Den Site Activity Patterns of Adult Male and Female Swift Foxes, 424
Vulpes velox, White Color Phase of the Swift Fox, 468
Vulpicida pinastri, 64
Vulture, Turkey, 11

Wagtail, Black-backed, 15
White, 15
Walde, A.D., J.R. Bider, C. Daigle, D. Masse, J.-C. Bourgeois, J. Jutras, and R.D. Titman. Ecological Aspects of a Wood Turtle, *Glyptemys insculpta*, Population at the Northern Limit of its Range in Québec, 377
Wallace, M.C., 645
Walleye, 542
Walnut, Black, 218
Wapiti, 196
Rocky Mountain, 197
Warbler, Arctic, 7
Black-throated Blue, 389
Blackpoll, 15
MacGillivray's, 7
Orange-crowned, 15
Palm, 15
Tennessee, 7
Townsend's, 7
Wilson's, 16
Yellow, 15,206,309
Yellow-rumped, 15
Warkentin, I.G., C.E. Campbell, K.G. Powell, and T.D. Leonard. First Record of Mink Frog, *Rana septentrionalis*, from Insular Newfoundland, 477
Washington, Black Bear, *Ursus americanus*, Denning Chronology and Den Site Selection in the Northeastern Cascades of, 626
Water-hemlock, Spotted, 296
Waterthrush, Northern, 15
Waxwing, Bohemian, 15
Cedar, 15,177
Weasel, Least, 18,245
Long-tailed, 193,246,313
Weasel, *Mustela frenata*, Hunting Behavior in Central West Virginia, Observations of Long-tailed, 313
Webster, W.D., 654
Wheatear, Northern, 15
Wheatgrass, Crested, 168,281
Intermediate, 283
Siberian, 281
Slender, 283
Tall, 283
Western, 25,168
Whimbrel, 13
White, J.D., 311

Whitefish, Lake, 59,642
Round, 59
Whitetop, 103
Whitlow-grass, 293
Lance-leaved, 293
Longstalk, 293
Yellowstone, 293
Whitman, J.S. Age Structure Differences in American Mink, *Mustela vison*, Populations under Varying Harvest Regimes, 35
Wiebe, M.O. and M.R. Lein. Response of Male Mountain Chickadees, *Poecile gambeli*, to Playback of Different Song Types, 76
Wiens, G., 123
Wigeon, American, 11
Eurasian, 11
Williams, A., 393
Williams, R., 634
Willis, C.K.R. and R.M. Brigham. New Records of the Eastern Red Bat, *Lasiurus borealis*, from Cypress Hills Provincial Park, Saskatchewan: A Response to Climate Change?, 651
Willow, 103,203
Alaska Bog, 289
Arctic, 289
Barren-ground, 289
Feltleaf, 289
Halbred, 289
Little-tree, 289
Mountain, 289
Northern, 289
Richardson's, 289
Round-leaf, 290
Snow-bed, 289,454
Variable, 289
Willowherb, Hornemann's, 296
Swamp, 296,461
Wilsonia pusilla, 16
Windels, S.K., 389
Wintergreen, Lesser, 296
Wisconsin, Death of Gray Wolves, *Canis lupus*, in Porcupine, *Erethizon dorsatum*, Dens in, 469
Wolf, 17,120,242,364,400,550,566
Alexander Archipelago, 7
Boreal Gray, 7
Gray, 7,357,419,468,469,589
Plains, 30
Red, 589
Wolf, *Canis lupus*, Pack Structure: Conservation Implications for Recovering Populations, Limits to Plasticity in Gray, 419
Wolf, *C. lupus* × *latrans* Hybrid Zone, Southeastern Ontario, Landscape Influence on *Canis* Morphological and Ecological Variation in a Coyote-, 589
Wolverine, 18,357,364,566
Wolves, *Canis lupus*, in Porcupine, *Erethizon dorsatum*, Dens in Wisconsin, Death of Gray, 469
Wood-Pewee, Western, 14
Wood-reed, Nodding, 282
Woodchuck, 7,247
Woodfern, Correll's, 651
Evergreen, 390
Woodpecker, Acorn, 311
Black-backed, 14
Downy, 14,179
Hairy, 14,177
Three-toed, 14
Woodrat, Bushy-tailed, 7
Woodsia alpina, 449
glabella, 449
ilvensis, 449
Woodsia, Northern, 451
Rusty, 451
Smooth, 451
Worm, Meningeal, 407
Wormwood, Northern, 463
Wren, Marsh, 169,654
Sedge, 348
Winter, 15
Wydeven, A.P., S.R. Boles, R.N. Schultz, and C.J.T. Doolittle. Death of Gray Wolves, *Canis lupus*, in Porcupine, *Erethizon dorsatum*, Dens in Wisconsin, 469

Xanthorion, 63
Xema sabini, 13

Yahner, R.H., 19
Yarrow, Woolly, 260
Yellow-toadflax, 298
Yellowlegs, Greater, 7
Lesser, 13
Yellowthroat, Common, 7
Yew, Canada, 389
Pacific, 215
Yew, *Taxus canadensis*, Small Mammal Abundance and Diversity in Forests with and without Canada, 389
Young, G.I. and R.H. Yahner. Distribution of, and Microhabitat Use by, Woodland Salamanders Along Forest-Farmland Edges, 19
Yucca glauca, 645
Yucca, Plains, 645
Yukon Territory V, New Records of Vascular Plants in the, 278

Zapus hudsonius, 6
princeps, 6
Zenaida macroura, 14,177
Zhang, T.Q., 267
Zonotrichia albicollis, 16,206
atricapilla, 16,206
capensis, 206
leucophrys, 16,203,617
leucophrys gambelii, 203
querula, 203
Zonotrichia leucophrys, in the Northwest Territories, Canada, Patterns of Nestling Feeding in Harris's Sparrows, *Zonotrichia querula* and White-crowned Sparrows, 203
Zonotrichia querula and White-crowned Sparrows, *Z. leucophrys*, in the Northwest Territories, Canada, Patterns of Nestling Feeding in Harris's Sparrows, 203
Zostera marina, 655

Index to Book Reviews

Botany

Blouin, G. An Eclectic Guide to Trees East of the Rockies, 497

Douglas, G.W., G.B. Straley, D. Meidinger and J. Pojar. Illustrated Flora of British Columbia Volumes 1-8, 329

Evans, C.L. The War on Weeds in the Prairie West: An Environmental History, 670

Kershaw, L. Ontario Wild Flowers, 330

Kirk, P.M., P.F. Cannon, J.C. David and J.A. Stalpers. Ainsworth and Bisby's Dictionary of the Fungi, 328

Lesica, P. A Flora of Glacier National Park, Montana, 159

Mitchell, R.S. and L. Danaher. Northeastern Fern Identifier, 669

More, D. and J. White. The Illustrated Encyclopedia of Trees, 496

Riley, J.L. Flora of the Hudson Bay Lowland and its Postglacial Origins, 669

Schnell, D.E. Carnivorous Plants of the United States and Canada: Second Edition, 496

Environment

Bierregaard, R.O. Jr., C. Gascon, T.E. Lovejoy, and R. Mesquita. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest, 672

DeGraaf, R.M. Trees, Shrubs, and Vines for Attracting Birds, 160

Dixon, T.F. City Wilds: Essays and Stories about Urban Nature, 498

Donovan, T.M. and C.W. Welden. Spreadsheet Exercises in Conservation Biology and Landscape Ecology, 506

Donovan, T.M. and C.W. Welden. Spreadsheet Exercises in Ecology and Evolution, 506

D'Orso, M. Plundering Paradise, 335

Ducey, J.E. Birds of the Untamed West: The History of Birdlife in Nebraska, 1750 to 1875, 336

Franklin, S.E. Remote Sensing for Sustainable Forest Management, 330

Frelich, L.E. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests, 502

Higgs, E. Nature by Design, 505

Johnsgard, P.A. Great Wildlife of the Great Plains, 504

Jones, H.G., J.W. Pomeroy, D.A. Walker and R.W. Hoham. Snow Ecology: An Interdisciplinary Examination of Snow-Covered Ecosystems, 332

Larson, D., U. Matthes, and P. Kelly. Cliff Ecology: Pattern and Process in Cliff Ecosystems, 672

Morris, W.F. and D.F. Doak. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis, 507

Nadkarni, N.M. and N.T. Wheelwright. Monteverde: Ecology and Conservation of a Tropical Cloud Forest, 334

Pullin, A.S. Conservation Biology, 499

Schwartzman, D. Life, Temperature, and the Earth, 498

Song, S.J. Ecological Basis for Stand Management: A Summary and Synthesis of Ecological Responses to Wildfire and Harvesting in Boreal Forests, 500

Suzuki, D. and A. McConnell. The Sacred Balance: A Visual Celebration of Our Place in Nature, 503

Thomashow, M. Bringing the Biosphere Home, Learning to Perceive Global Environmental Change, 159

Watt, A. The Last Island: A Naturalist's Sojourn on Triangle Island, 505

Wiese, F. Seabirds and Atlantic Canada's Ship-Source Oil Pollution, 332

Miscellaneous

Arnaudin, M.P. A Bird in the Bush: The Story of the Province of Quebec Society for the Protection of Birds 1917-2002, 508

Baker, D.B. John Keast Lord: Materials for a Life, 338

Berry, M.F. The Dinosaur Filmography, 341

Browne, J. Charles Darwin, The Power of Place, 340

Debus, A.A. and D.E. Debus. Paleoimagery, The Evolution of Dinosaurs in Art, 341

Hodgson, B. Naturalists: A Journal, 342

Hodgson, B. Women Travelers: A Journal, 342

King, J. Farley: The Life of Farley Mowat, 509

Lawrence, R.D. The North Runner, 674

Nicklen, P. and H. Brody. Seasons of the Arctic, 674

Stroud, P.T. The Emperor of Nature: Charles-Lucien Bonaparte and his World, 337

Suzuki, D. When the Wild Comes Leaping Up: Personal Encounters with Nature, 339,675

Zoology

Barter, M.A., Shorebirds of the Yellow Sea: Importance, Threats and Conservation Status, 321

Behnke, R.J. Trout and Salmon of North America, 318

Brooks, R.J., D. Strickland, and R.J. Rutter. Reptiles and Amphibians of Algonquin Provincial Park, 490

Byers, J.A. Built for Speed: A Year in the Life of Pronghorn, 661

Catling, P.M., C.D. Jones and P. Pratt. Ontario Odonata. Volume 3 (including observations for the year 2001), 487

Clements, J.F. Birds of the World: A Checklist, 322

Collette, B.B. and G. Klein-MacPhee. Bigelow and Schroeder's Fishes of the Gulf of Maine, 319

del Hoyo, J., A. Elliott, and J. Sargatal. Handbook of Birds of the World. Volume 8: Broadbills to Tapaculos, 663

Downer, J. Weird Nature: An Astonishing Exploratioin of Nature's Strangest Behavior, 158

Eder, T. Mammals of Ontario, 487

Ernst, C.H. and E.M. Ernst. Snakes of the United States and Canada, 495

Fishpool, L.D.C. and M.I. Evans. Important Bird Areas in Africa and Associated Islands: Priority Sites for Conservation, 664

Gittleman, J.L., S.M. Funk, D. MacDonald, and R.K. Wayne. Carnivore Conservation, 155

Halliday, T. and K. Adler. Firefly Encyclopedia of Reptiles and Amphibians, 327

Heintzelman, D. All-Weather Hawk Watcher's Field Journal, 326

Holman, J.A. In Quest of Great Lakes Ice Age Vertebrates, 494

Houston, C.S. and W. Anaka. Birds of Yorkton – Duck Mountain, 668

Jaramillo, A. Birds of Chile, 659

Jones, K.A. Knowing Bass: The Scientific Approach to Catching More Fish, 156

Kays, R.W. and D.E. Wilson. Mammals of North America, 488

Knott, D.L. A Spring Expedition to the Falkland Islands and Antarctica, 320
Lacey, E.A., J.L. Patton, and G.N. Cameron. Life Underground, the Biology of Subterranean Rodents, 157
Leverton R. Enjoying Moths, 327
Lieske, E. and R. Myers. Coral Reef Fishes: Indo-Pacific and Caribbean – Revised Edition, 662
Love, M.S., M. Yoklavich and L. Thorsteinson. The Rockfishes of the Northeast Pacific, 323
Manly, B.J., L.L. McDonald, D.L. Thomas, T.L. McDonald and W.P. Erickson. Resource Selection by Animals, 325
Matthiessen, P. The Birds of Heaven: Travels with Cranes, 158
Maxwell, B.A., J.K. Werner, P. Hendricks, and D.L. Faith. Herpetology in Montana: A History, Status Summary, Checklists, Dichotomous Keys, Accounts of Native, Potentially Native, and Exotic Species, and Indexed Bibliography, 491
Mecklenburg, C.W., T.A. Mecklenburg, and L.K. Thorsteinson. Fishes of Alaska, 151
Riede, K. Global Register of Migratory Species (GROMS): Database, GIS Maps, and Threat Analysis, 154
Rossi, J. and R. Rossi. Snakes of the United States and Canada: Natural History and Care in Captivity, 666
Russell, C. and M. Enns. Grizzly Heart: Living without Fear among the Brown Bears of Kamchatka, 662
Saffron, I. Caviar: The Strange History and Uncertain Future of the World's Most Coveted Delicacy, 324
Scott, J.M., S. Conant and C. Van Riper III. Evolution, Ecology, Conservation, and Management of Hawaiian Birds: A Vanishing Avifauna, 153
Shirihai, H. The Complete Guide to Antarctic Wildlife, 489
Sibley, D.A. Sibley's Birding Basics, 151
Szczerbak, N.N. Guide to the Reptiles of the Eastern Palearctic, 492
Taylor, P. The Birds of Manitoba, 660
Urquhart, E. and A. Bowley. Stonechats: A Guide to the Genus Saxicola, 667
Zug, G.R., L.J. Vitt, and J.P. Caldwell. Herpetology: An Introductory Biology of Amphibians and Reptiles, Second Edition, 493

Extralimital sighting of a Polar Bear, *Ursus maritimus*, in northeast Saskatchewan
MICHAEL A. GOODYEAR 648

Dryopteris goldiana × *D. intermedia*, a natural fern hybrid new to Canada PAUL M. CATLING 649

New records of the Eastern Red Bat, *Lasiurus borealis*, from Cypress Hills Provincial Park, Saskatchewan: A response to climate change? CRAIG K. R. WILLIS AND R. MARK BRIGHAM 651

Marsh Rice Rat, *Oryzomys palustris*, predation on Forster's Tern, *Sterna forsteri*, eggs in coastal North Carolina JOHN H. BRUNJES IV AND WM. DAVID WEBSTER 654

Documenting Pronghorn Antelope, *Antilocapra americana*, in the Peace River grasslands, Alberta THERESA A. FERGUSON 657

Book Reviews

ZOOLOGY: Birds of Chile — The Birds of Manitoba — Built for Speed: A Year in the Life of Pronghorn — Coral Reef Fishes: Indo–Pacific and Caribbean Revised Edition — Grizzly Heart: Living without Fear among the Brown Bears of Kamchatka — Handbook of Birds of the World. Volume 8: Broadbills to Tapaculos — Important Bird Areas in Africa and Associated Islands: Priority Sites for Conservation — Snakes of the United States and Canada: Natural History and Care in Captivity — Stonechats: A Guide to the Genus Saxicola — Birds of Yorkton – Duck Mountain 659

BOTANY: Northeastern Fern Identifier — Flora of Hudson Bay Lowland and its Postglacial Origins — The War on Weeds in the Prairie West: An Environmental History 669

ENVIRONMENT: Cliff Ecology: Pattern and Process in Cliff Ecosystems — Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest 672

MISCELLANEOUS: The North Runner — Seasons of the Arctic — When the Wild Comes Leaping Up: Personal Encounters with Nature 674

NEW TITLES 675

News and Comment

Point Pelee Natural History News 3(3) — *Froglog*: Newsletter of the Declining Amphibian Populations Task Force (59, 60) — *Amphibian Voice* Summer 2003 — Marine Turtle Newsletter (102) — Recovery Strategy for Bowhead Whales in Canadian Eastern Arctic — National Recovery Strategy for Species at Risk in the Sydenham River: An Ecosystem Approach — *Recovery*: An Endangered Species Newsletter (25) 677

The Ottawa Field–Naturalists' Club Awards for 2002 679

Index to Volume 117 COMPILED BY LESLIE CODY 681

Mailing date of the previous issue 117(3): 12 July 2004

Articles

Canopy interception of acid deposition in southern Ontario
JULES CARLSON, WILLIAM A. GOUGH, JIM D. KARAGATZIDES, AND LEONARD J. S. TSUJI 523

Comparison of the ground vegetation in spruce plantations and natural forest in the Greater Fundy ecosystem, New Brunswick
CAM VEINOTTE, BILL FREEDMAN, WOLFGANG MAASS, AND FRIEDERIKE KIRSTEIN 531

Movement of Lake Sturgeon, *Acipenser fulvescens*, in a natural reach of the Ottawa River
TIM HAXTON 541

An aerial survey technique for the forest-dwelling ecotype of the Woodland Caribou, *Rangifer tarandus*, in Quebec REHAUME COURTOIS, ANDRE GINGRAS, CLAUDE DUSSAULT, LAURIER BRETON, AND JEAN–PIERRE OUELLET 546

Subtidal hydroids (Cnidaria) of Northumberland Strait, Atlantic Canada, with observations on their life cycles and distributions DALE R. CALDER 555

Seasonal habitat use and movements of Mountain Goats, *Oreamnos americanus*, in east-central British Columbia KIM G. POOLE AND DOUGLAS C. HEARD 565

Planispiral burrows from a Recent lacustrine beach, Gander Lake, Newfoundland
ROBERT B. MACNAUGHTON 577

Have Lesser Scaup, *Aythya affinis*, reproductive rates declined in parkland Manitoba?
DAVID N. KOONS AND JAY J. ROTELLA 582

Landscape influence on *Canis* morphological and ecological variation in a Coyote–Wolf, *Canis lupus* × *latrans*, hybrid zone, southeastern Ontario HILARY J. SEARS, JOHN THEBERGE, MARY T. THEBERGE, IAN THORNTON, AND DOUGLAS CAMPBELL 589

Bald Eagles, *Haliaeetus leucocephalus*, feeding on spawning on Plainfin Midshipman, *Porichthys notatus*, at Crescent Beach, British Columbia
KYLE HAMISH ELLIOTT, CHRISTINA L. STRUIK, AND JOHN E. ELLIOTT 601

Do female Northern Pintails, *Anas acuta*, initiate rapid follicular growth during spring migration?
PASCALE DOMBROWSKI, JEAN–CLAUDE BOURGEOIS, RICHARD COUTURE, AND CHRISTIAN LINARD 605

Supposed periodicity of redpoll, *Carduelis* sp., winter visitations in Atlantic Canada
ANTHONY J. ERSKINE AND REID MCMANUS, JR. 611

Methods for capturing free-ranging Black Bears, *Ursus americanus,* in difficult locations
JOHN E. MCDONALD, JR. 621

Black Bear, *Ursus americanus*, denning chronology and site selection in the northeastern Cascades of Washington WILLIAM L. GAINES 626

First report of a sea louse, *Lepeophtheirus salmonis*, infestation on juvenile Pink Salmon, *Oncorhynchus gorbuscha*, in nearshore habitat ALEXANDRA B. MORTON AND ROB WILLIAMS 634

Notes

First record of the Deepwater Sculpin, *Myoxocephalus thompsonii,* from George Lake in Whiteshell Provincial Park, Manitoba L. MURRAY, M. H. PAPST, AND J. D. REIST 642

Coyote, *Canis latrans* – Rio Grand Turkey, *Meleagris gallopavo intermedia*, interactions
BRIAN L. SPEARS, WARREN B. BALLARD, MARK C. WALLACE, ROGER D. APPLEGATE, AND PHILLIP S. GIPSON 645

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 01115 3848

ISSN 0008-3550

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 01226 6201

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 01481 6342